主論文

Phenology and wasp population dynamics of several species of dioecious fig in a lowland tropical rain forest in Sarawak, Malaysia

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"The Fici of Borneo show quite a series of adaptations, both in their shape and size, to varied biological conditions, and well deserve special investigation"

Odoardo Beccari (1904), *Wanderings in the Great Forests of Borneo*

Center for Ecological Research, Kyoto University,

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"There is genuine paradox and real poetry lurking in the fig, with subtleties to exercise an enquiring mind and wonders to uplift an aesthetic one...But the fig is only one out of millions that all have the same Darwinian grammar and logic – albeit the fig story is amongst the most satisfyingly intricate in evolution."

Richard Dawkins (1996), *Climbing Mount Improbable*

"But amongst the squatters grow more sinister, and ultimately murderous plants. They are the figs."

David Attenborough (1995), *The private life of plants*

"Every fruit has its secret

the fig is a very secretive fruit"

D. H. Lawrence, *The Fig*

Abstract

The phenology of several dioecious figs and the population dynamics of their pollinating and non pollinating wasps were studied, with respect to climatic variability and sexual specialisation, at Lambir Hills National Park, Sarawak (4^0 20' N, 113^0 50' E, 150 – 250 m above sea level), over a four year period from October 1994. Figs and their pollinating wasps have evolved a unique seed predator/pollinator interaction, in which the fig wasps in return for pollination services raise their offspring in the fig inflorescence. In dioecious species different plants specialise in seed production or in pollinator wasp and pollen production, the female and male roles respectively. The high specificity of the fig – fig wasp interaction and the short adult life-span of pollinators tightly couples the production of fig inflorescences to the population dynamics of their pollinators, making this system an ideal subject for investigating the impact of climatic variability on plant – animal interactions. Wide variation in phenological strategies was demonstrated in the three main species studied. Leaf production increase following periods of drought, although all three species, and especially *Ficus cereicarpa*, produced new leaf continuously. However, in *F. cereicarpa* and *F. schwarzii*, both cauliflorous species, leaf production was not correlated to the production of inflorescences. By contrast, *F. fulva* flushed both new leaf and inflorescences simultaneously on the same young twigs. There was no sexual specialisation in leaf production. Differences between species in reproductive phenology were more pronounced. All showed increased production of inflorescences following droughts, however, *F. cereicarpa* produced inflorescences asynchronously within an individual, and this buffered wasp production against the disruptive effects of minor droughts. *F. schwarzii* produced highly synchronous crops at short intervals and even minor droughts caused populations to become synchronised, inducing persistent oscillations in pollinator production. Because of these effects the population size of figs had little influence on the stability of the pollinator populations. Pollinator and non pollinator populations sampled at receptive trees were strongly correlated to the production of wasps within the local fig patch. Non pollinator populations, however, were more severely affected by minor droughts. The pollination success of figs also reflected the production of wasps in the local patch, suggesting fig patches were semi-isolated populations. *F. fulva* had a synchronous phenology similar to *F. schwarzii*, but the inter-crop interval wàs longer and trees did not appear so adversely affected by minor droughts. Sexual specialisation was investigated in *F. fulva* and demonstrated in; the duration of crop development, crop size, crop investment profile, the ability of male trees to provide their own pollinators, and growth strategy. These results led me to suggest that these phenological strategies are adaptive to an aseasonal climate and not seasonal climates as has been claimed in other species. During the very severe drought in 1998, induced by the 1997/98 El Niño Southern Oscillation event, the pollinating wasps of dioecious figs became locally extinct at Lambir Hills National Park and in all but one species did not re-invade for at least six months. This evidence for the breakdown of interactions between species has serious implications for the maintenance of biodiversity if the predictions of increasing frequency and severity of droughts driven by global warming are borne out.

Contents

1 Introduction

1.1 Tropical forests in South East Asia

The tropical forests of South East Asia are the most diverse terrestrial ecosystem on Earth and have existed since at least the Tertiary (Whitmore 1984). Their antiquity and the favourableness of a permanently humid climate for plant growth and year round reproduction were previously supposed to be responsible for the development of their extraordinary biological diversity. However, more recently the perception of these forests as bastions of stability has been considerably eroded. As recently as the Pleistocene glaciations several major climatic and sea-level fluctuations took place which led to corresponding advances and retreats of the forests (Whitmore 1981; Flenley 1998). Even over ecological time-scales catastrophic disturbances, such as drought, fire, volcanic eruptions, typhoon and land-slides, have been recorded (Thornton 1984; Whitmore 1984; Ashton 1993; Thornton 1996). Of particular interest in recent years has been the impacts of global climatic oscillations, such as the El Niño Southern Oscillation (ENSO), and how these are being affected by global warming (Cane & Zebiak 1985; Leighton & Wirawan 1986; Woods 1989; Webster & Palmer 1997; Salafsky 1998; Kudo & Kitayama 1999; Nakagawa *et al. in press*). Such rare but severe disturbances are clearly very important in the ecology of these forests yet our understanding of them remains fragmentary. Moreover, in recent decades primary forests have been pushed back into smaller and ever more isolated patches with the expansion of human populations, the intensification of agriculture and logging. The survival of a large part of the biodiversity of tropical regions will thus largely depend on the extent to which these small reserves are able to withstand occasional catastrophic disturbances (Whitmore 1984; Ashton 1993; Turner *et al.* 1997; Bawa & Dayanandan 1998; Nepstad *et al.* 1999).

Many animals depend directly on plant resources for sustenance, and even in the aseasonal tropical regions the availability of these resources varies in time and space (van Schaik 1986; Wright & Cornejo 1990; Wright 1991; van Schaik *et al.* 1993; Reich 1995; Corlett & Lafrankie 1998). The populations of herbivores, pollinators, seed predators and seed dispersers in a forest thus depend on plant behaviour in terms of the timing of growth or leaf flushing and flowering or fruiting (Janzen 1974; Wolda 1978; Murray *et al.* 1987; Wolda 1988; Aiello 1992; Brody 1997; Wright *et al.* 1999; Roubik *in prep*). Conversely, the fluctuation of herbivore, pollinator, seed predator and seed disperser populations will influence plant fitness and hence the evolution of plant behavioural strategies (Janzen 1976; Augspurger 1980; Augspurger 1981; Augspurger 1983; Aide 1988; Richards 1990; Marquis 1992; Rodriguez *et al.* 1992; Aide 1993; Balasubramanian 1996). Just as in the famous 'entangled bank' described by Darwin (1859), it is in these co-evolved interactions, the silk yarns of the web of life, that the rain forest resides. How they are affected by the vagaries of climate, and how resistant they may or may not be to catastrophic disturbance, in a landscape drastically changed by recent human activities, will determine to a large degree the nature of the community that survives into the next millennium (Condit *et al.* 1996; Bawa & Dayanandan 1998; Condit 1998; Nepstad *et al.* 1999).

1.2 Natural history of figs

1.2.1 Background

Figs (*Ficus* spp., Moraceae) are an ancient group of plants believed to have evolved from the proto-ficus during the Cretaceous, approximately 100 million years ago (Murray 1985; Collinson 1989). Today they are one of the most diverse tropical genera with over 750 species world-wide (Berg 1989), and in Malaya no other genus compares to the figs in the sheer abundance of individuals nor in their diversity of habits, which range from stranglers (hemi-epiphytes), climbers, epiphytes, and understory shrubs, to small and large trees (Corner 1940). Figs are also primarily a tropical genus, with only a few species reaching temperate latitudes (Berg 1989). A unique pollination system, high species diversity, individual abundance, and the importance of fig fruit for wildlife (Terborgh 1986; Lambert & Marshall 1991) make figs one of the most interesting genera in tropical forests (Janzen 1979b).

1.2.2 Pollination and the fig – fig wasp mutualism

All figs have a closed urn shaped inflorescence, or syconium, which when receptive is lined with tiny uniovulate female flowers (Fig. 1-1A & B). Species specific pollinating fig wasps (Fig. 1-1A (insert)) (Agaonidae, Chalcidoidea, Hymenoptera) are attracted to the syconia by a specific bouquet of volatile chemicals (Jennings 1977; Barker 1985; Ware *et al.* 1993; Hossaert McKey *et al.* 1994; Ware & Compton 1994; Gibernau *et al.* 1997) and enter through the bracts of the narrow entrance, or ostiole, losing their wings and antennae in the process. Co-evolution between the fig and pollinator has led to a specific architecture of ostiole bracts which is unlocked by the head shape of the wasp, rather like a lock and key (Verkerke 1989; Van Noort & Compton 1996). Once inside the fig wasps pollinate the flowers and, by inserting their ovipositors down the styles, attempt to oviposit on the ovules (Galil & Eisikowitch 1968; Galil & Eisikowitch 1969; Galil 1973; Beck & Lord 1988b). In monoecious figs style length has a continuous distribution and the wasps' ovipositors can reach most ovules (Verkerke 1988; Ganeshaiah *et al.* 1995; Nefdt & Compton 1996).

Ovules which receive an egg are induced to form a gall on which the wasp larvae feeds, while those which are missed by the wasp, if pollinated, develop into seed normally. Several weeks later the new adult male wasps emerge and mate the females still enclosed in their galls within the syconium. The wingless males then cut a tunnel, often through the ostiole, and die. Meanwhile, the females collect pollen from the now mature male flowers, which may simply involve a passive dusting or the active filling of pollen pockets (Fig. 1-1E) (Ramirez 1968; Galil & Meiri 1981; Joseph & Abdurahiman 1981; Ramirez & Malavasi 1997), and depart in search of a receptive syconium (Fig. 1-1F) (Galil 1977). A few days later the fruits ripen and are eaten by a diverse assortment of vertebrate seed dispersers (Janzen 1979b; Coates Estrada & Estrada 1986; Shanahan & Compton *in press*), from reptiles (Whiting & Greeff 1997) and fish (Horn 1997) to bats (August 1981; Funakoshi *et al.* 1993; Kalko *et al.* 1996; Tan *et al.* 1998), birds (Jordano 1983; Lambert 1989b; Lambert & Marshall 1991; Compton *et al.* 1996; Athreya 1997), primates (Figueiredo 1993; Palombit 1997) and other mammals (Lopez Forment & Urbano 1979; Lambert 1990; Heydon & Bulloh 1997),

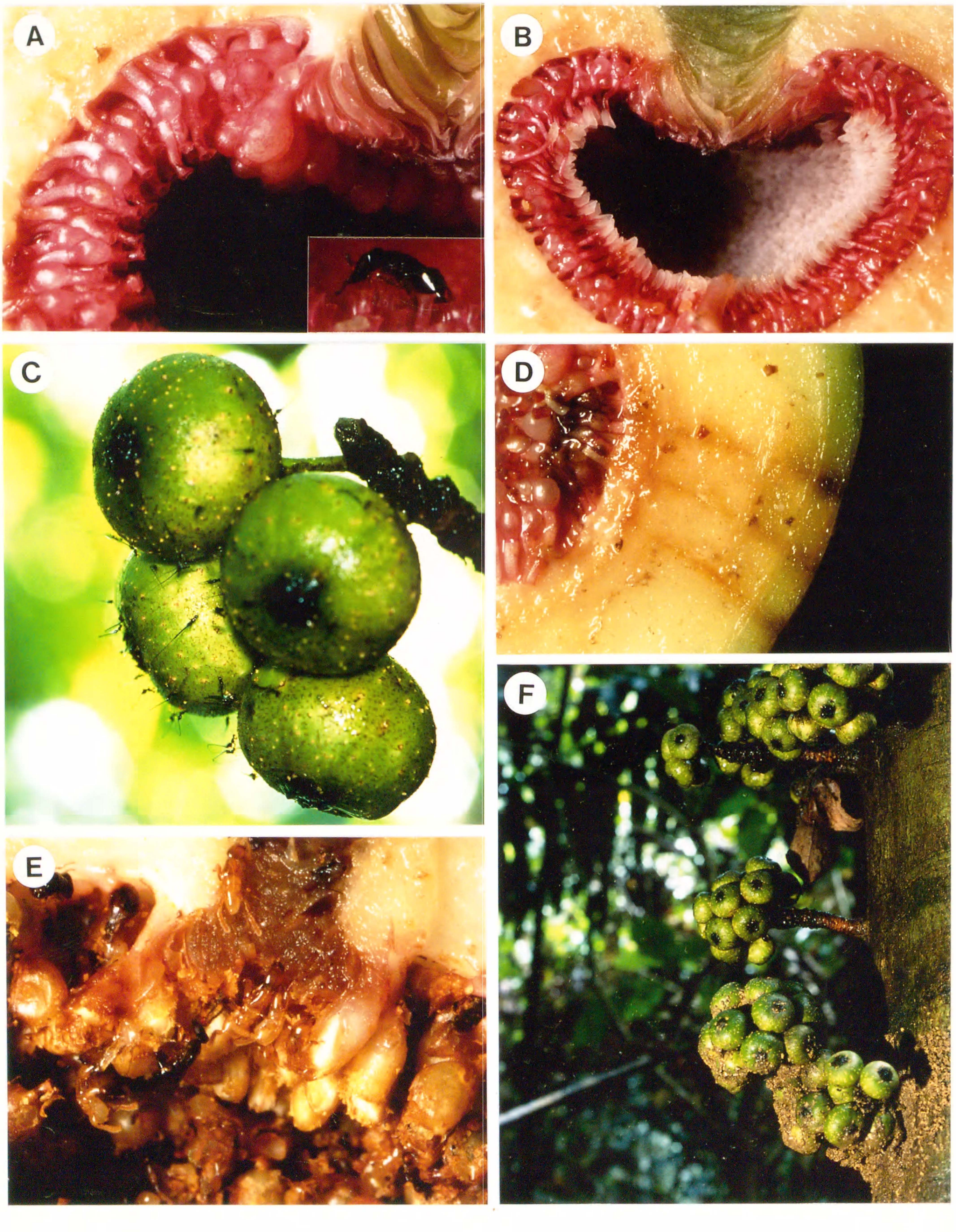

Figure 1-1

Figure 1-1 Natural history of the fig – fig wasp interaction. A: Cross-section of a receptive male syconia of *F. schwarzii* showing two rows of immature male flowers around the ostiole bracts and the modified female flowers with cup shaped stigmas adapted to receive a wasp's ovipositor. Insert: Pollinating wasp, having lost its wings and antennae while entering the ostiole bracts, is scrambling over the stigmas ovipositing and unloading pollen. B: Cross-section of a female syconia of *F. schwarzii* showing the female flowers with long styles and flat, bificated stigmas adapted to receive pollen. The syconia is in the late immature stage with the ostiole bracts still tightly closed. C: Non pollinators of the genus *Philotrypesis* ovipositing through the syconia wall with their long ovipositors. D: Damage caused by the ovipositors of non pollinators. This is a female syconia, however, and hence the non pollinators failed to lay any eggs although they still damages some ovaries. E: Interior of a male syconia at the emergence phase. Light coloured, wingless male wasps are starting to cut a tunnel up through the ostiole while a darker, female wasps is loading pollen its pollen pockets from the now mature male flowers. F: Continuing the cycle, pollinators arriving in clouds at receptive syconia (specks of light are the flash reflecting off the wings of the wasps). Adult female wasps have very short life spans, usually less than one day, and hence must find a receptive tree almost immediately if they are to reproduce successfully.

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often with secondary seed dispersal by ants (Roberts & Heithaus 1986; Kaufmann *et al.* 1991).

In dioecious figs the system is similar to monoecious figs but there are two types of tree, bearing different syconia (Beck & Lord 1988a). Female trees have syconia with long, thin styled female flowers (Fig. 1-1B). Pollinating wasps enter but fail to lay eggs because their ovipositors are unable to penetrate down the styles and reach the ovules. They therefore die without reproducing but are unable to avoid female syconia (Patel *et al.* 1995). Male trees bear syconia with short styled 'female' flowers (gall flowers) and male flowers (Fig. 1-1A). The pollinating wasps are able to oviposit in all ovules and no seed is produced (see Kjellberg *et al.* 1987b for exception in *F. carica*). Female trees thus produce only seed, while male trees produce pollen and pollinators (Galil 1973; Beck & Lord 1988b). Formerly dioecious figs were often referred to as gynodioecious (eg Corner 1965; Patel 1996) reflecting the fact that the short styled flowers in male syconia which are galled by the pollinators are derived from female flowers. However, the term is inappropriate as they have lost their female function of producing seed and the sexual system is clearly dioecious.

During the emergence fig wasps are prone to ant predation. In some species the wingless male wasps cut a wide tunnel and then scatter across the surface of the syconia, a behavior which permits the rapid escape of the female wasps while the ants are distracted into collecting the male wasps (Harrison 1996).

1.2.3 Fig wasps as seed predators

The closed inflorescence of figs prevents any other pollinators from reaching the flowers. Fig wasps, too, are unable to raise their offspring outside the syconium of their particular fig species. The relationship can thus be described as an obligate mutualism – meaning both partners are entirely dependent of the other to complete their life cycles. It is in fact possibly one of the most intricate relationships found in nature. However, the interests of the fig and fig wasp are not completely aligned (Kjellberg *et al.* 1987b). The fig wasp is a seed predator. For each pollinator larvae raised one ovule is destroyed and hence the fig pays for it with one less seed (Janzen 1979a; Bronstein 1992; Nefdt & Compton 1996). Like most 'mutualisms' it is more a case of mutual exploitation than co-operation (Leigh & Rowell 1995; Doebeli & Knowlton 1998; Herre 1999a). The fig wasp would clearly benefit from producing more offspring at the expense of fig seeds, while the fig should wish to maintain an approximately even investment in pollinators and seed (Charnov 1982). In dioecious figs, wasps have no reproductive interest in entering female syconia. That they cannot discriminate between female and male syconia (Patel *et al.* 1995), and that the number of ovules used for seed and wasp production is roughly even in monoecious figs (Nefdt & Compton 1996; Herre & West 1997), indicates the figs apparently have the upper hand in this co-evolutionary exploitation. On the other hand, it is not in the interests of the fig to produce male wasps as only the females carry pollen to the next fig tree. Hence, fig trees should benefit from maintaining a strongly female biased sex ratio through local mate competition (Hamilton 1979). In this case it is the fig wasps that appear to maintain control at least within a single syconium where the sex ratios closely reflect the number of foundresses. However, overall the sex ratio is female biased suggesting figs control the mean number of pollinators that can enter a syconium through proximate mechanisms that are not well understood (Herre 1985; Herre 1987; Herre 1989). The subtle ways in which the fig – fig wasp mutualism appears to resolve these conflicts, which appears more often than not to reflect proximal control and fortuitous pre-adaptation than complex co-evolutionary mechanisms, is one of the most interesting and active areas of fig research (Kjellberg *et al.* 1987a; Bronstein 1988b; Nefdt & Compton 1996; Herre & West 1997; West & Herre 1998; Herre 1999a).

Given the obvious conflict of interests it is not surprising to find that mutualistic seed predator – pollinator interactions are rare in nature (Pellmyr 1997) having only truly developed in the Yuccas and Yucca moths (Udovic 1981; Udovic & Aker 1981; Addicott 1986; Pellmyr & Tompson 1992; Thompson & Pellmyr 1992; Pellmyr & Huth 1994; Addicott & Tyre 1995; Huth & Pellmyr 1997), and possibly some Cycads and Rhopalotria beetles (Norstog *et al.* 1986; Tang 1987; Norstog & Fawcett 1989; Donaldson 1997), Senita cactus- senita cactus moth, *Trollius europeaeus* and *Chiastocheta* flies (Pellmyr 1997) besides the figs and fig wasps.

1.2.4 Specificity of the fig – fig wasp interaction

The fig – fig wasp interaction is one of the most specific found in nature (Ramirez 1970; Ramirez 1974; Wiebes 1979). For almost every species of fig there is a one to one relationship with the fig wasp pollinator (see Wiebes 1979 for exceptions). Despite the fact that fig communities are often composed of a diverse array of widely dispersed species (Hubbell & Foster 1986; Harrison *unpublished data*) breakdowns in specificity are incredibly rare and usually involve the artificial introduction of figs outside their natural range (Ramirez & Montero 1988; Emygdio 1990; Ware & Compton 1992). Even captures of wrong species of fig wasps in the crown of a fig are remarkably rare. For example Bronstein (1987) found that 99% of individual fig wasps arriving at sticky traps were of the appropriate species. The volatile search cues (Jennings 1977; Barker 1985; Ware *et al.* 1993; Hossaert McKey *et al.* 1994; Ware & Compton 1994; Gibernau *et al.* 1997) and physical barriers of the fig surface and especially the ostiole (Verkerke 1989; Van Noort & Compton 1996) are obviously very efficient.

1.2.5 Non pollinating fig wasps

A suite of closely related, also highly species specific (Machado *et al.* 1996), non pollinating wasps (gallers, gall parasites and parasitoids) (Boucek *et al.* 1981; Ulenberg & Nubel 1982; Compton & Nefdt 1990; Compton *et al.* 1991; Compton & van Noort 1992; West & Herre 1994; Kerdelhue & Rasplus 1996b), most of whom oviposit through the syconia wall using very long ovipositors (Abdurahiman & Joseph 1979; Ulenberg & Nubel 1982), also raise their larvae in the fig syconia. In dioecious figs they are only recorded from male syconia, another words those which raise pollinator larvae. Non pollinating wasps are essentially parasites of the fig – fig wasp mutualism and have a negative impact on the fig through resource utilisation, especially seed predation, and through their impact on pollinating wasps (West & Herre 1994; Kerdelhue & Rasplus 1996b). By essentially imitating the pollinating wasps and sheltering behind the investment the fig has in a syconium with seed and pollinator larvae already developing, the non pollinators generally appear to have evaded the evolution of counter measures. In at least one species of dioecious fig, syconia that are heavily parasitised early in their development are aborted (Harrison 1996) and several species of fig have evolved secondary mutualisms with ants which patrol the surfaces of syconia preying on non pollinators while they are ovipositing (Compton & Robertson 1988; Harrison 1996; Cushman *et al.* 1998). The employment of ants, however, is a double edged sword as ants are also efficient predators of the pollinating wasps especially at the emerging phase, but also when arriving at receptive syconia (Bronstein 1988c). The outcome of the interaction hence often depends on the particular ant species present (Dejean *et al.* 1997) and on avoidance behaviour by the pollinators, such as the males acting as decoys during the emergence (Harrison 1996).

1.2.6 Internal parasites of fig wasps

To further complicate the story, internal parasites of the fig wasps, both pollinators and non pollinators (Vovlas & Larizza 1996), also influence the evolutionary outcome of the fig – fig wasp interaction. Nematodes reduce the fitness of pollinating wasps but their virulence is dependent on the degree of vertical transmission, which is a corollary of the mean number of pollinator foundresses that enter a syconium for a particular fig species (Herre 1993; Herre 1995). *Wolbachia*, intra-cellular bacteria which are transmitted maternally and modify the hosts reproduction to suit their own transmission (Cook & Butcher 1999), are also found in fig wasps (Herre, *personal communication*). Their influence on the sex ratio of the wasps and their degree of vertical verses horizontal transmission has yet to be investigated.

1.2.7 Fig phenology

Studies of plant phenology examine the timing and frequency of recurring biological events, such as the production of flowers and fruit or maintenance activities such as leaf renewal. As mentioned above, the populations of organisms dependent on plants for resources, such as herbivores, pollinators or seed dispersers, are affected by the temporal variation in these resources caused by plant phenology. These biotic factors also in turn affect phenological schedules of plants, as do climatic and other abiotic factors (reviewed in van Schaik *et al.* 1993; Brody 1997). At least for some species it has been shown that plant reproductive success is correlated with phenological traits (e.g. Augspurger 1981; Aide 1988; Rodriguez *et al.* 1992).

The aseasonal lowland Dipterocarp forests of SE Asia are famous for their large scale community flowering events in which 50% or more of the individuals in a forest may flower after three or more years of little or no reproductive activity (Wood 1956; Burgess 1972; Medway 1972; Ng 1977; Ashton *et al.* 1988; Momose *et al.* 1998a; Momose *et al.* 1998b; Sakai *et al. in press*; Harrison *et al. in press*). In contrast, the constraint of maintaining the pollinator populations prevents such long inter-flowering intervals at the population level in figs (Bronstein *et al.* 1990; Anstett *et al.* 1997; Kameyama *et al. in press*).

The unique biology of figs, thus, permits a detailed examination of many of these climatic and biotic factors and how in turn they may affect subtle balances in the fig – fig pollinator mutualism. Previous studies have largely concentrated on monoecious figs (eg Milton *et al.* 1982; Bronstein 1988a; Damstra *et al.* 1996; Herre 1996) or on dioecious figs in relatively strongly seasonal environments (eg Hill 1967; Valdeyron & Lloyd 1979; Kjellberg *et al.* 1987a; Patel 1996; Spencer *et al.* 1996; Patel & McKey 1998). There is therefore interest in investigating the phenology of figs, especially dioecious figs, in an aseasonal environment where regular climatic cues are absent but occasional climatic phenomena, especially droughts, occur.

The classic reproductive phenology of figs involves the production of large highly synchronous crops on individual trees but asynchrony in flowering between individuals (eg Janzen 1979b; Bronstein 1988a; Bronstein *et al.* 1990; Patel 1996; Spencer *et al.* 1996). Synchrony within the individual may be explained by physiological constraints, and selection for a large cohort size to attract pollinators and seed dispersers. Avoidance of self-pollination (Janzen 1979b; Bronstein *et al.* 1990; Milton 1991; Bronstein & Patel 1992) may also play a role in monoecious figs though it seems insufficient to explain the degree of synchrony, which generally separates the receptive and male phase of a crop by two or more weeks, and the long inter-crop intervals normally observed. In fact, given the higher fruiting frequency of larger individuals (Milton 1991) resource limitation combined with selection for a large optimal crop size would appear to be key. Asynchrony between individuals may be maintained by independent, and variable (Milton 1991), endogenous rhythms and an environment with unpredictably fluctuating pollination and seed dispersal opportunities (Milton *et al.* 1982; Milton 1991). Maintenance of the fig wasp population although often mentioned (Bronstein *et al.* 1990; Milton 1991) requires group level selection and given the large sizes of genetically interacting populations (Bronstein *et al.* 1990; Nason *et al.* 1998) seems unlike to be important.

Breakdowns in this classical phenology through synchrony between individuals (Damstra *et al.* 1996; Smith & Bronstein 1996) or asynchrony within an individual (Bronstein 1989; Patel 1996) have been recorded in certain special situations. Synchrony between individuals is generally induced by strongly seasonal environments (van Schaik 1986; Damstra *et al.* 1996; Patel 1996; Smith & Bronstein 1996; Spencer *et al.* 1996) while asynchrony within individuals by seasonality (Cook & Power 1996; De Figueiredo & Sazima 1997) and/or a poor pollination environment (Bronstein 1989; Bronstein & Patel 1992).

Although this classical fig phenology appears to apply to many species, especially amongst monoecious figs, other types of phenology exist. Possibly the best known is that of *F. carica* the cultivate fig of the Mediterranean which has a regular series of syconia cohorts tied to the seasons, including a small over-wintering crop (Valdeyron & Lloyd 1979; Kjellberg *et al.* 1987a). *F. erecta* (Thumb), a non-cultivated species in Japan, appears to have a very similar phenology (Harrison, *personal observation*). Perhaps less specialised but nonetheless different types of phenology such as within individual asynchronous syconia production (Corlett 1993; Patel 1996) or more rapid production of smaller crops (Corlett 1987) have also been recorded. Hence, there is considerable variation in the types of phenology evidenced in figs and it may be anticipated that these different types will be related to a suite of environmental characters including the climate, local habitat conditions, and the ecology of the pollinators and seed dispersers. Therefore, by comparing the phenology of fig species in relation to their environment we may gain useful insights into their ecology, and by extension that of the other organisms associated with them. Furthermore, the unique biology of figs permits a detailed examination of how these various environmental factors may affect their reproductive success and that of their pollinators, unravelling a little more of the mystery of the fig –fig wasp interaction (Herre 1996; Nefdt & Compton 1996; Herre 1999b).

1.2.8 Fig wasp population dynamics

Adult female pollinators have extremely short life spans (Kjellberg *et al.* 1988; De Figueiredo & Sazima 1997), many live less than a day (Harrison, *unpublished data*). Hence, they are dependent on the availability of receptive syconia (male syconia for dioecious figs) when they emerge to reproduce successfully. Conversely, pollination success of fig trees is dependent on the production of adult pollinators (Bronstein 1988a). Syconia are able to wait a few weeks for pollinators (Khadari *et al.* 1995; Anstett *et al.* 1996) but they are eventually aborted if there is no pollination. The high specificity of the fig – fig pollinator interaction and a short adult life-span for the wasp, therefore, tightly couples fig wasp populations to fig phenology. At the population level, figs must exhibit a phenology in which syconia are produced almost continuously, so that the pollinator population is able to cycle from one cohort of syconia to the next, either on the same tree or on neighbouring trees. A substantial gap in the production of syconia, for longer than the total duration of wasp life-span (1 – 2 months depending on the species) would lead to the extinction of the fig wasp population (Bronstein *et al.* 1990; Kameyama *et al. in press*). It is the continuous availability of fig fruit, especially when other more seasonal fruits are not to be found, that makes figs so incredibly valuable for vertebrate seed dispersers (Terborgh 1986; Lambert 1989a; Lambert & Marshall 1991; Tan *et al.* 1998; Shanahan 1997).

The populations of non pollinating wasps are also linked to the production of syconia (on male trees for dioecious figs). Non pollinators often live considerably longer that the pollinators though still not more than a week or two (Compton *et al.* 1994a; Harrison, *unpublished data*). How the populations of non pollinators respond to variable syconia availability, and especially how they compare to the pollinators, may reveal interesting aspects to their ecology and how this differs with respect to their trophic level or guild. Moreover, study of the population dynamics of the non pollinators, particularly when controlled for variation between crops and between syconia within a crop, can reveal the impact of non pollinators on the production of pollinators and/or seed, and hence the cost of these 'parasites' to the fig (West & Herre 1994; Kobbi *et al.* 1996).

1.3 Study Site

In Lambir Hills National Park (LHNP), Sarawak (4^0 20' N, 113^0 50' E, 150 – 250 m above sea level, Fig. 1-2) the vegetation types is generally described to as lowland dipterocarp forest (Ashton 1995) due to the dominance of this family in the canopy and emergent layers. The forest is typified by extraordinary high trees species diversity, with over 1200 species in a 52 ha plot within the park (LaFrankie *et al.* 1995), and a very high canopy and emergent layer (35 – 80 m). Two basic soil types occur within the park, with ridge tops dominated by drier humults and valleys by wetter udults. Many tree species, including figs (Harrison *in prep*), segregating more or less strictly

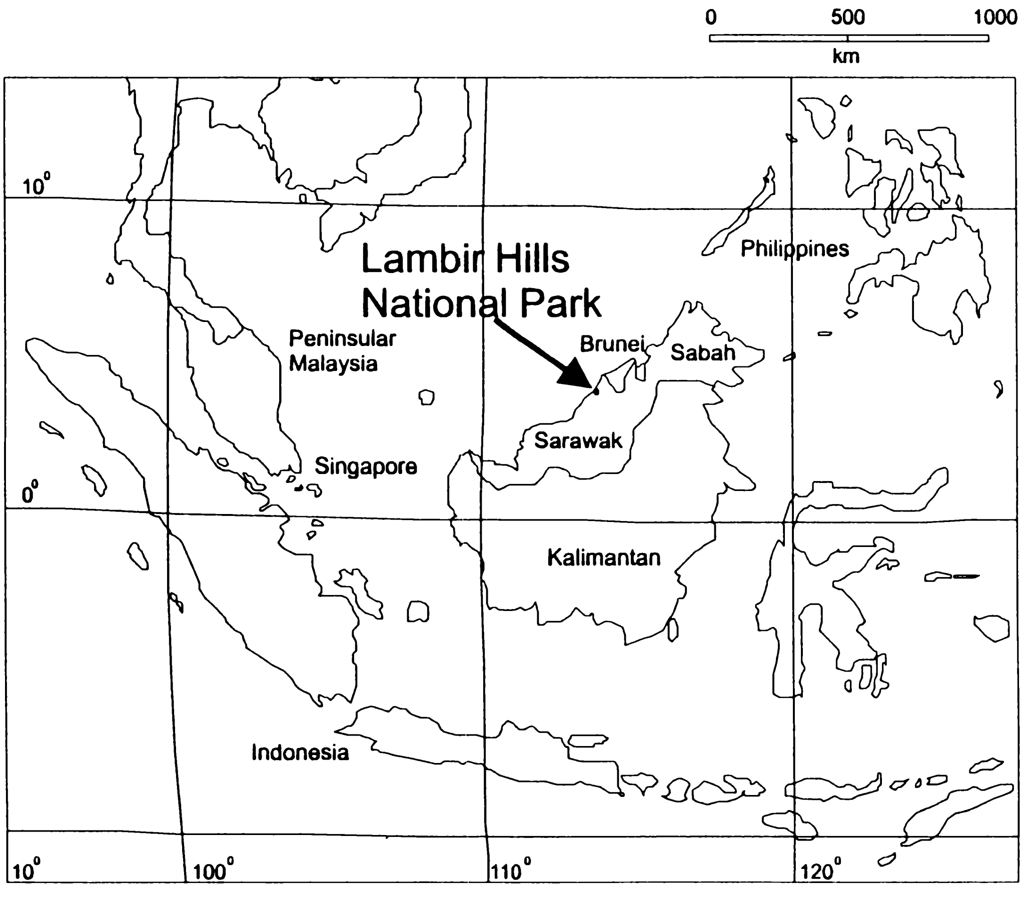

Figure 1-2 Map of South East Asia showing the location of Lambir Hills National Park

according to soil type (Ashton 1995; Itoh *et al.* 1995; Itoh *et al.* 1997). LHNP is approximately 6 500 ha. Commercial pressure has reduced this forest type throughout the region so that only a few small fragments remain such as here and in Brunei (Cranbrook & Edwards 1994).

Studies were located in the primary forest in and around the Canopy Biology Plot (Inoue & Hamid 1994) at LHNP and in secondary forest at the Lupong Aji longhouse approximately 5 km East of the park headquarters.

1.4 Climate

Within the tropics, where the daily temperature range is often more than the annual variation in month mean temperature, it is rainfall and especially the length of the dry season that determines the distribution of forest types (Whitmore 1998). The central South East Asian tropics experience a year round equatorial warm climate with high rainfall and no predictable dry season (Whitmore 1984). At LHNP mean annual temperature is 26^0C while daily temperature ranges from a minimum of about 23^0C to a maximum of about 32^0C. Mean annual precipitation is approximately 2700 mm, with monthly average precipitation ranging from 167.5 mm in July to 328.4 mm in November (Nakagawa *et al. in press*; Harrison *in submission*). Wet monsoons from the Indian Ocean in summer and the Pacific Ocean in winter bring rain at all times of year. Nevertheless, rainfall is highly variable and extended dry periods of a month or more occur occasionally, usually when one or other of the monsoons is delayed due to the irregular movements of the Intertropical Convergence Zone (Brunig 1969; Baillie

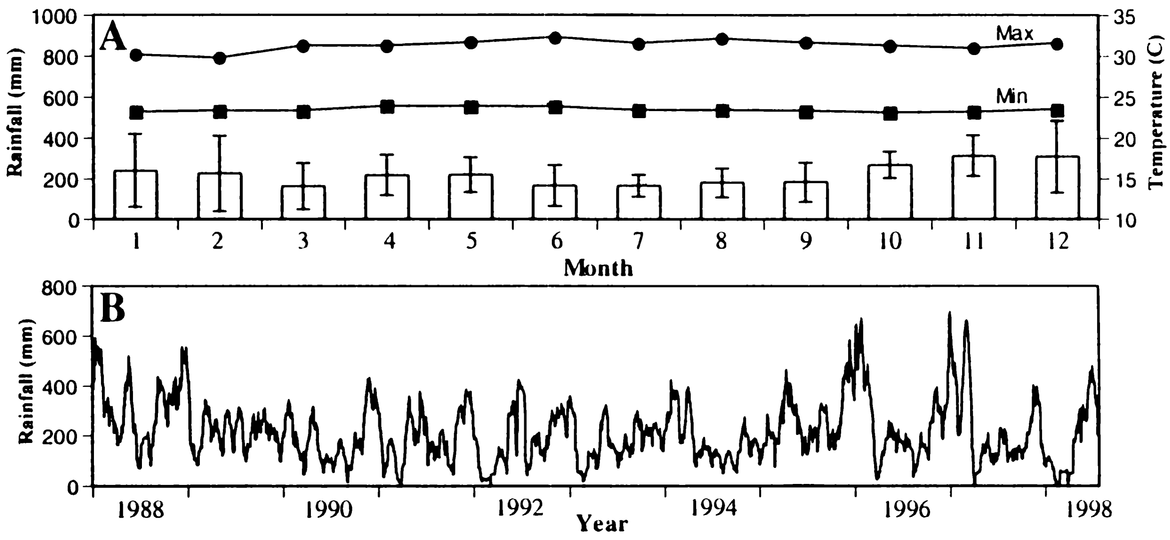

Figure 1-3 Temperature and rainfall records (1967 –1999) from Miri Airport, approximately 30 km north of Lambir Hills National Park. A: Mean monthly minimum and maximum temperature and mean monthly rainfall (+/- standard deviation). The climate is warm year round with little variation in temperature. Mean monthly rainfall is also relatively even around the year and there are no obvious dry months (mean monthly rainfall <100 mm, Whitmore 1984). B: 30-day rolling rainfall totals clearly show that rainfall is highly variable from one period to the next and that minor droughts, at least, are not rare (Brunig 1969).

1976; Cranbrook & Edwards 1994). Rainfall in the north of Sarawak is more equitable than around Kuching but annual rainfall is lower so that in fact this area experiences more dry periods (Brunig 1969; Harrison *in submission*).

Rainfall records (1967 – 1999) from Miri Airport (Fig. 1-3) 30 km north of LHNP show that brief periods of drought (30 day rainfall total <100 mm, Brunig 1969; Whitmore 1984) occur in almost every 12 month period, or a total of 108 times in the 32 year period. Minor droughts are not therefore rare and occur most often in February – March, before the onset of the southern monsoon, or sometimes again in August – September before the onset of the monsoon off the Pacific (Seal 1957; Brunig 1969; Baillie 1976). Even droughts which lasted for two or more months occurred 15 times and more intense droughts, in which the 30 day total dropped below 10 mm, occurred nine times. However, most droughts are slight (Fig. 1-3).

Severe droughts are rare and usually associated with El Niño Southern Oscillation Events (ENSO) (Fig. 1-3 & Fig 1-4). ENSO events occur when the pool of warm surface water normally located in the western Pacific region breaks out and flows back eastwards shutting off the cool upwelling currents off the coast of South America causing flooding over the land, while reduced evapotranspiration in the western Pacific leads to droughts over South East Asia and Australia (Gill & Ramusson 1983; Cane & Zebiak 1985; Webster & Palmer 1997; Guilderson & Schrag 1998). The biological impacts of this climatic anomaly are substantial (Barber & Chavez 1983; Woods 1989; Condit *et al.* 1995; Huppert & Stone 1998; Kudo & Kitayama 1999; Wright *et al.* 1999; Nakagawa *et al. in press*; Harrison *in submission*).

Since about 1966 there has been an increase in the frequency and severity of the droughts associated of El Niño events (Webster & Palmer 1997; Guilderson & Schrag 1998; Huppert & Stone 1998) which as led to a corresponding increase in the occurrence and severity of droughts associated with them in Borneo (Fig. 1-4; Salafsky 1998). It was previously suggested (Walsh 1996) that the latest spate of droughts simply reflected long term periodic changes in frequency with an earlier episode of severe droughts evident between about 1877 and 1915 in Sandakan, north-east Borneo. Rainfall data was not collected from the Miri area prior to 1912, however, the tail end of this earlier episode is recorded in the droughts of 1915, which was not strong in Miri, 1919 and 1923. Nevertheless, the droughts of the past two decades do appear extraordinary (Fig 1-4).

Given the periodicity of ENSO appears to have remained stable for over 100 000 years (Pearce 1999) and that the climate models are predicting that global warming will increase the frequency and severity of ENSO (Meehl 1997; Timmermann *et al.* 1999), it would seem complacent to assume that something more than simple long term variability is not afoot.

By far the strongest drought was that associated with the recent 1997-98 ENSO event when the 30 day rolling rainfall total remained below 10 mm for more two months (Fig. 1-3 & Fig. 1-4). Nakagawa (1999) compared the 3-month-shifting-average rainfall from the 1967-1999 period to a log normal distribution and found droughts of the intensity of 1998 can be expected roughly every 360 years. When

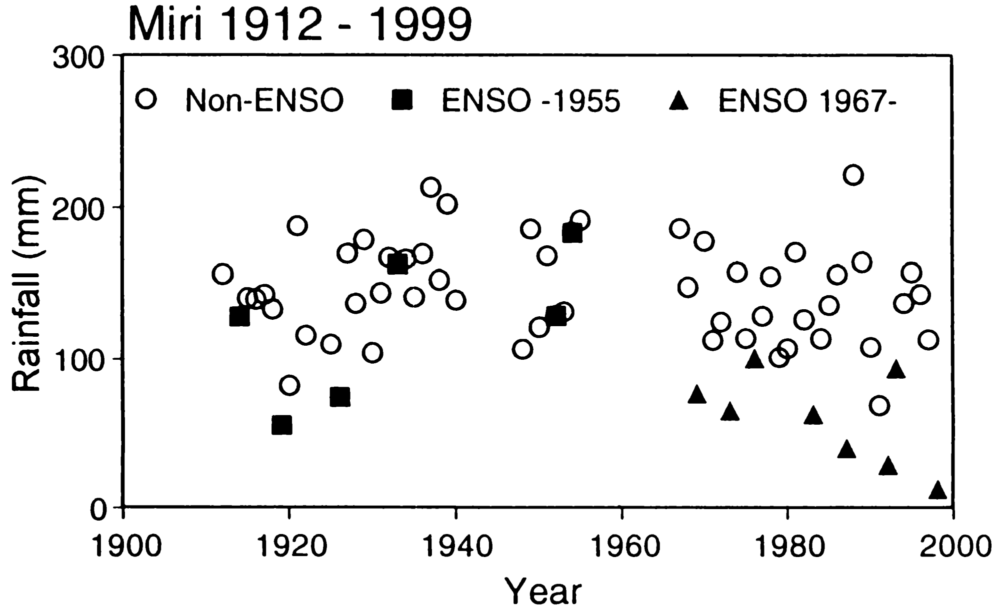

Figure 1-4 Incidence of droughts in the Miri area since 1912. The yearly minimum 3-month-shifting-average-rainfall is plotted (data from Seal 1957 prior to 1967). ENSO years are indicated. The incidence and severity of droughts has clearly increase in the past two decades.

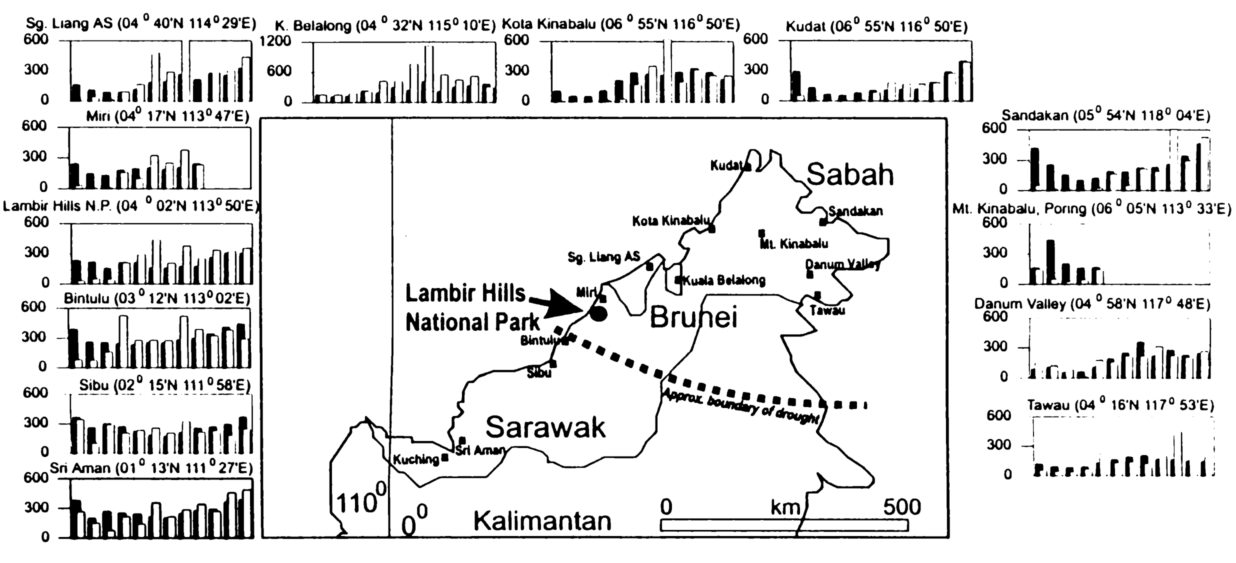

Figure 1-5 The area affected by the severe drought in early 1998. Filled bars indicate the long term mean monthly rainfall and empty bars the rainfall for 1998. The entire northern region of Borneo suffered from the drought, though some areas particularly those near large areas of undisturbed forest (compare Belalong FSC with Sg. Liang AS in Brunei) were less severely affected.

records back to 1912 are used the expected frequency of a drought as severe as that in 1998 is even lower, less than once per 1000 years (Harrison *in submission*).

The 1997/98 drought was also very widespread affecting the entire northern region of Borneo (Fig. 1-5). The fact that severe droughts affect very wide areas, as compared to other disturbances such as wind-throw or fire, is an important aspect to their impact on the natural ecosystems. It also has major implications for the conservation of biodiversity given the high levels of endemism in many taxa and the aforementioned fragmentation of the remaining forest reserves.

We can conclude then that minor droughts are common but very severe droughts are rare and usually associated with ENSO events. In recent decades ENSO events have become more frequent and more severe and the droughts associated with them much more severe. Severe droughts also have an impact over very wide areas.

1.5 Purpose of study

1.5.1 General purpose

The purpose of this study was to investigate the influence of climatic variability, especially drought, on the phenology of several dioecious figs at LHNP, and to see how fluctuations in the resources available to fig wasps affected their population dynamics, and how this in turn influenced the reproductive success of figs.

The specialised inflorescence of figs and their unique seed predator – pollinator pollination system means all species of figs have a remarkably conservative reproductive ecology which makes figs an ideal subject for comparative studies (Bronstein & McKey 1989; Herre 1996). As mentioned earlier, fig phenology varies often widely amongst species hence I followed the phenology of several species and compared how the differing phenology of each species responded to climatic fluctuation. Furthermore, as dioecious figs have male and female roles segregated on separate trees it was possible to investigate how sexual specialisation had fashioned phenology, which in turn points to the selection pressures acting on either wasp production or seed production.

Finally, in discussing the impacts of the severe drought in 1998 I draw implications for the maintenance of biodiversity under a scenario of increasing frequency and severity of droughts driven by global warming.

1.5.2 The studies

In Chapter Two I examine the interaction of climate, fig phenology and wasp population dynamics in two species of dioecious fig at LHNP. These species were selected because while there are phylogenetically closely related, both belonging to subgenus *ficus* section Sycocarpus, and are found at the same sites, their phenological characteristics are clearly quite different. Leaf phenology as a simple maintenance activity might be expected to respond directly to climatic variability. While, on the other hand, syconia production should reflect sexual selection and the constraints of the fig – fig wasp mutualism, in addition to the influences of climate. Hence my focus was on;

a) temporal variation in the production of leaf and syconia, in relation to climate and especially drought, in small and large patches of each fig species,

b) how patch size influenced the population stability of the pollinating and non pollinating wasps, and

c) how the population dynamics of the wasps affected the pollination success of male and female trees.

In Chapter Three I investigate the influence of climate, especially rainfall, and sexual specialisation on the phenology of a common roadside fig, *Ficus fulva*, at LHNP. This species being an abundant, open space tree was easily observed and, because it belongs to different section (Ficus) provided an interesting comparison to the species studied in Chapter Two. In this study the focus was on;

a) how leaf and reproductive phenology were influenced by climatic variability, especially drought, and

b) the sexual specialisation of phenology and how this reflected the selection pressures acting on the wasp and seed production.

In Chapter Four I investigate the impact of the severe drought in 1998 on the stability of fig wasp populations at LHNP, and discuss the implications for the maintenance of biodiversity under a scenario of worsening and more frequent droughts driven by global warming.

2 Phenology and wasp population dynamics of two dioecious figs in a lowland tropical forest in Sarawak

Summary

The phenology of two dioecious figs (*Ficus cereicarpa* and *F. schwarzii*) and populations dynamics of their species specific pollinating and non pollinating fig wasps were studied at LHNP. Small and large patches of each fig species were studied in relation to climate, especially drought, between Nov 1994 and Oct 1998. *F. cereicarpa* individuals produced syconia asynchronously, which buffered against the effects of minor droughts. In contrast, *F. schwarzii* individuals produced frequent synchronous crops with asynchrony between trees. Normally, this maintained a high stable production of pollinators but even minor drought severely disrupted the phenology. Trees became synchronized, which led to persistent peaks and crashes in pollinator production. The population dynamics of pollinators and non pollinating wasps reflected wasp production in the local populations, and pollination success was also correlated to local pollinator production.

2.1 Introduction

Studies of plant phenology examine the timing and frequency of recurring biological events, such as the production of flowers and fruit or maintenance activities such as leaf renewal. The populations of organisms dependent on plants for resources, such as herbivores, pollinators or seed dispersers, are affected by the temporal variation in these resources caused by plant phenology. These biotic factors also in turn affect phenological schedules, as do climatic and other abiotic factors (van Schaik *et al.* 1993; Reich 1995; Brody 1997). Reproductive success may thus be correlated with phenological traits (Augspurger 1981; Augspurger 1983; Richards 1990). The unique biology of figs permits a detailed examination of many of these factors, because the short adult life and high specificity of the pollinators tightly couples fig phenology with pollinator, and non pollinator, population dynamics. Moreover, with the sexual roles segregated on different trees dioecious figs offer the chance to examine phenology with respect to sexual function (Cox 1981; Cox 1982; Richards 1990).

In temperate regions clear annual cycles of plant phenology predominate, where reduced biological activity in winter moulds patterns, and figs are no exception (Valdeyron & Lloyd 1979; Kjellberg & Maurice 1989). In tropical regions periodic change in rainfall generally determines seasonality (van Schaik *et al.* 1993). Dry seasons occur in most tropical regions and many studies have shown correlations between plant phenology and rainfall (e.g. Augspurger 1981; Borchert 1983; van Schaik 1986; Wright & Cornejo 1990; Wright 1991; Borchert 1994; Borchert 1998). Even in figs, which are obliged to fruit year round in order to maintain their pollinator populations, there may be seasonal fluctuations in syconia production (Milton *et al.* 1982; Windsor *et al.* 1989; Milton 1991; Damstra *et al.* 1996, for monoecious; Hill 1967; Patel 1996; Spencer *et al.* 1996; Patel & McKey 1998 for dioecious). The central part of South East Asia, lacks a predictable dry period and is essentially aseasonal. However, occasional droughts do occur and these are implicated in having a major impact on the ecology of forests in the region (Whitmore 1984; Ashton 1993). LHNP, therefore, offers the opportunity to examine dioecious fig phenology in what is perhaps the most aseasonal environment yet investigated, but one in which irregular periods of climatic stress occur.

In diverse tropical forests species exist at low mean densities but for figs a certain threshold population is necessary to maintain the pollinator populations (Bronstein *et al.* 1990; Kameyama *et al. in press*). Monoecious figs solve this conundrum by having pollinators which disperse long distances (Nason *et al.* 1996; Nason *et al.* 1998). An alternative solution is to stabilise pollinator production in smaller populations, which dioecy permits through a rapid turnover of syconia on male trees – de-coupled as it is from seed development of which is generally much slower (Corlett 1987; Corlett 1993; Patel & McKey 1998; Chapter 3). However, this would only be stable in an aseasonal climate where there is temporally even selection for pollinator and seed production. Hence, I suggest that dioecious figs evolved to the existence of small, semi-isolated populations in aseasonal climates (Kameyama *et al. in press*). Although it is not possible to develop a simple hypothesis, this does lead to the following predictions; (1) syconia production should be even throughout the year on both male and female trees, (2) individuals should exist in small relatively isolated populations but (3) periods of stress, i.e. drought, are expected to have a substantial impact on the stability of pollinator populations.

Contrary to these ideas, it has been suggested that dioecy in figs may have evolved in response to seasonality (Kjellberg & Maurice 1989) and that observed phenologies in a tropical seasonal environment may be adaptive (Patel 1996; Spencer *et al.* 1996). Hence, it is interesting to see whether these interpretations stand up to the examination of dioecious fig phenology in an aseasonal environment but one in which unpredictable periods of plant stress occur.

In this study I examined the interaction of fig phenology and wasp population dynamics in two species of dioecious figs at LHNP. In particular I focused on;

a) temporal variation in the production of leaf and syconia, in relation to climate and especially drought, in small and large patches of each fig species,
b) how patch size influenced the population stability of pollinating and non pollinating wasps, and
c) how this in turn affected the pollination success of male and female trees.

2.2 Materials and Methods

2.2.1 Species and Study Site

Ficus cereicarpa Corner and *F. schwarzii* Koord (Subgenus *Ficus*, sect. *Sycocarpus*) (Corner 1965) are both cauliflorous, dioecious figs. *F. cereicarpa* is endemic to northern Borneo. It is a small pioneer tree (3 – 8 m), which bears syconia (4 – 8 cm diameter) in tight spiral bunches on short, stout branchlets. Syconia within a bunch are synchronous but there is asynchrony between bunches. It is pollinated by *Ceratosolen pilipes* Weibes (Wiebes 1963) and has one undescribed non pollinating fig wasp, *Sycoscapter* sp., a gall parasite (Boucek *et al.* 1981). The seed dispersers are large rats. *F. schwarzii* is distributed from Myam Mar and Thailand to Sumatra, Borneo and Sulawesi. It is a medium sized (15 – 20 m) pioneer tree. Syconia (2 – 3 cm diameter) are borne from the trunk on thin branchlets. Crops are generally very synchronous but with overlap between the tails of crops especially on female trees. It is pollinated by *Ceratosolen vetustus* Wiebes (Wiebes 1994) and has three species of undescribed non pollinating wasp, *Apocryptophagus* sp., a galler, *Philotrypesis* sp., a gall parasite, and *Apocrypta* sp., a parasitoid (host not known) (Boucek *et al.* 1981, Harrison 1996). Fruits of *F. schwarzii* are dispersed by small fruit bats. Both species can be found on the same sites though *F. cereicarpa* apparently prefers damper ground.

The first site (Swamp) observed from Nov 1994 – Oct 1998 was located in partially disturbed forest within LHNP. The second site (Longhouse) observed from Jun 1996 – Oct 1998 was located in the secondary forest near the Rumah Aji longhouse, approximately 5 km from the first site. Both sites were selected to encompass small patches of both species and the surrounding forest was searched to locate outlying individuals. At the Longhouse some outliers not included in the censuses certainly existed in the extensive secondary forest around the site. Furthermore, as we have no information concerning the dispersal abilities of the wasps, the sites are not assumed to be single populations but their degree of isolation will be addressed later in the paper.

Rainfall data for the park for the period 1988 – 1998 was obtained from the Telecom Malaysia tower located in the park, while temperature data for the period 1991 – 1998 was obtained from Miri Airport 30 km from the research site. Referring to the study period from 1995 (Fig. 1-3) onwards it can be seen that brief droughts occurred in Mar 1996 and Mar 1997 with a very severe drought from Jan – Apr 1998. The drought in 1996 occurred after four years without drought.

2.2.2 *Field observation*

At the Swamp (*F. cereicarpa*:18-female, 9-male; *F. schwarzii*:10-female, 13-male, 1-immature) censuses were started in Nov 1994 and to Jun 1995 were conducted every week. From Jul 1995 to May 1996 they were conducted monthly. Then from Jun 1996 – Oct 1998 they were conducted every 10 days. Two *F. cereicarpa* male were not included in the census until Jun 1996, while one *F. cereicarpa* female, three *F. schwarzii* female and one male died during the first year. At the Longhouse (*F. cereicarpa*:33-female, 36-male, 9-immature; *F. schwarzii*:28-female, 22-male) censuses were initiated in Jun 1996 for *F. schwarzii* and in Aug 1996 for *F. cereicarpa* and conducted every 10 days until Oct 1998.

At each census amount of leaf, as a proportion of the crown, and proportion of new leaf, old leaf and senile leaf were recorded using a 1 – 4 scale (1 <25%, 25>2<50%, 50%>3<75%, 4>75%). Number of syconia were estimated on a log scale with three sub-groupings, thus 1 – 3, 4 – 6, 7 – 9, 10 – 39, 40 – 69 and so on. The proportion of syconia at each developmental stage was estimated on a similar 1 – 4 scale to the leaf data. Crop developmental stage was assigned as Immature, Receptive, Pollinated and Fruit/Mature Male (Galil 1973). Where there were sufficient syconia in a crop the stage was assessed by sampling a small number (3 – 5). However, often this was not possible and crop stage had to be assessed by visual appearance, and other evidence such as the presence of pollinator wings in the ostiole bracts or non pollinator wasps on the surface. Tree size and growth, and factors such as crown illumination were measured, however, this paper deals only with population level phenomena.

At the Swamp from Jan 1995 – Jun 1995 and again from Jun 1996 – Mar 1998 yellow sticky traps were hung singly in most trees (First period: *F. cereicarpa* n=10, *F. schwarzii* n=25; second period: *F. cereicarpa* n=12, *F. schwarzii* n=18) to sample wasp arrivals. On male trees they were removed during the male phase of a crop cycle. The traps were made of plastic drainage pipe approximately 10 cm diameter and 30 cm long (ca. 950 cm^2) and sprayed yellow (Bronstein 1987). They were painted with Tanglefoot which was renewed as required. The traps were checked over a 5 day sampling period and this was maintained as continuously as possible throughout the two trapping periods (First period 18 censuses, second period 78 censuses). Wasps were identified and counted on the traps, then cleaned off for the next census.

2.2.3 *Data analysis*

Data were analysed using *SAS* (*SAS Institute Inc* 1985, PROC SUMMARY, PROC NPAR1WAY and PROC CORR). I calculated the proportions of trees with new leaf and syconia at different developmental stages; total number of syconia at each stage; and total number of wasps of each species caught, for each census. These data were compared using non parametric tests. To test between years or first and second periods of intensive study at the Swamp, or between species, or sites I compared the means and variance by quarter. For correlations between parameters along the time series I used data by census. Delayed correlations between parameters and auto-correlations were investigated. Periods of intensive census were either analysed separately from monthly censuses or the first census date in each month was used. The numbers of wasps on sticky traps were summed over two censuses to make the interval comparable to the phenology censuses and when correlations between sites were conducted census dates within five days of one another were compared. Data from the trees which died at the Swamp were used in all analysis except for comparisons between years, and drought and non drought periods. Data after Feb 1998 were not used to eliminate the drastic effects of the drought in that year.

2.3 Results

2.3.1 Leaf Production

The proportion of trees with new leaf present was very variable from one month to the next (Fig. 2-1) but the mean proportion of trees with new leaf did not differ across years (*F. cereicarpa*: x^2=3.96, df=2, p>0.05, *F. schwarzii*: x^2=4.88, df=2, p>0.05. Kruskal-Wallis test, 1998 excluded) or between sites for either species (*F. cereicarpa* s=19, z=-1.67, p>0.05, *F. schwarzii* s=61, z=1.02, p>0.05, Wilcoxon two sample test, 1998 excluded). During the severe 1998 drought all trees lost all or most of their leaf which was then renewed with the onset of rainy weather (Fig. 2-1). *F. cereicarpa* individuals were only occasionally recorded flushing, defined as when >25% of the crown consisted of new leaf, but often with new leaf present, while *F. schwarzii* trees flushed sporadically but was recorded with new leaf less often. Comparing the timing of leaf production between sites, species and sexes (Table 2-1) most parameters showed highly significant correlations. In fact only flushing compared between sites, in both species, and between species at the Swamp showed non significant relationships. However, from auto-correlation analysis neither species showed any consistent periodicity in leaf production at the population level.

2.3.2 Syconia Production

The proportion of trees with pollinated syconia (Fig. 2-2) is a good indicator of syconia production because it is a measure which incorporates all stages of development of seed or pollinator larvae, and its distribution across the population.

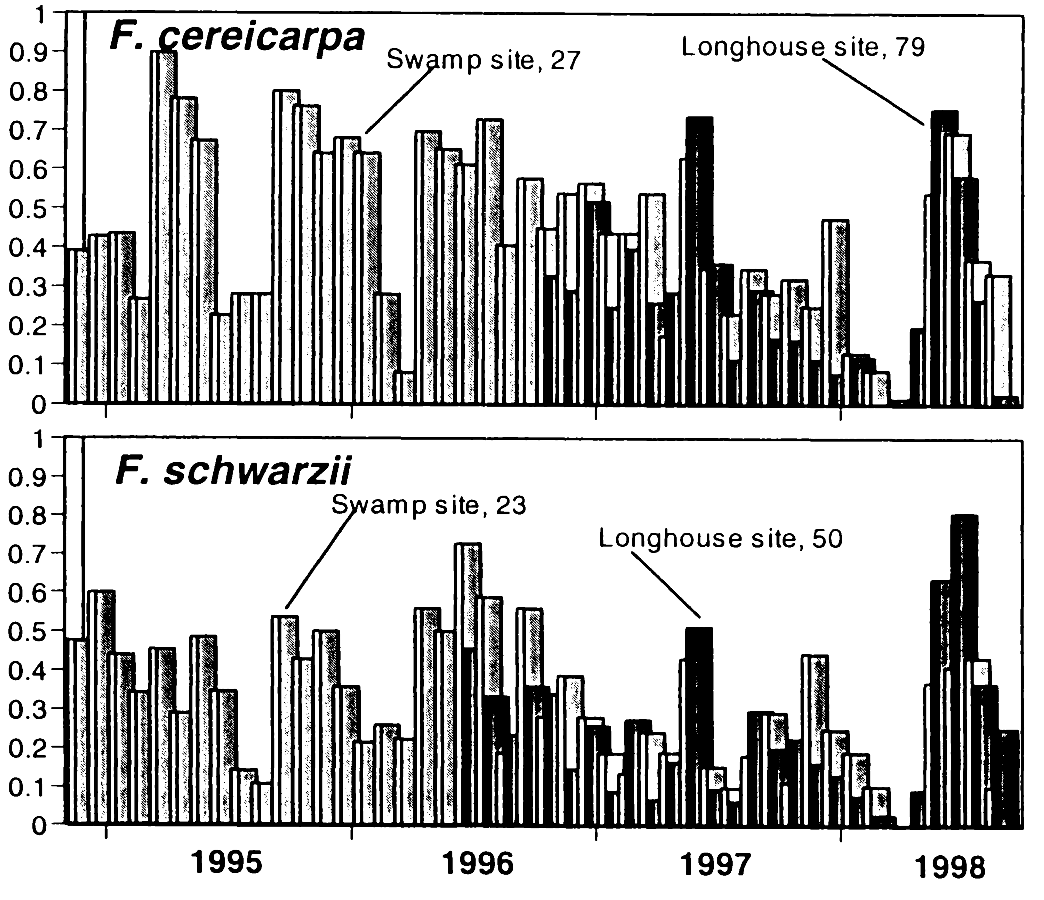

Figure 2-1 Mean proportion of trees with new leaf by month for *F. cereicarpa* and *F. schwarzii* in a small population (Swamp), Nov 1994 – Jul 1998, and a large population (Longhouse), Jun 1996 – Jul 1998.

Table 2-1 Correlations in the timing of leaf production for *F. cereicarpa* and *F. schwarzii* at two sites. Data on the proportion of trees with new leaf present (New Leaf) and with >25% of the crown consisting of new leaf (Flushing) at each census were compared by Kendall Rank Correlation, *tau* compared to a normal distribution (data after Feb. 1998 not included).

Between sites		*F. schwarzii*	*F. cereicarpa*
	New leaf	0.431***	0.573***
	Flushing	0.247 ns	0.167 ns
Between species		Longhouse site	Swamp site
	New leaf	0.494***	0.322**
	Flushing	0.433**	0.154 ns
Between sexes		Longhouse site	Swamp site
F. schwarzii	New leaf	0.758***	0.485***
	Flushing	0.597***	0.495***
F. cereicarpa	New leaf	0.800***	0.401***
	Flushing	0.627***	0.359**

(ns p>0.05, * p<0.05, ** p<0.01, *** p<0.001)

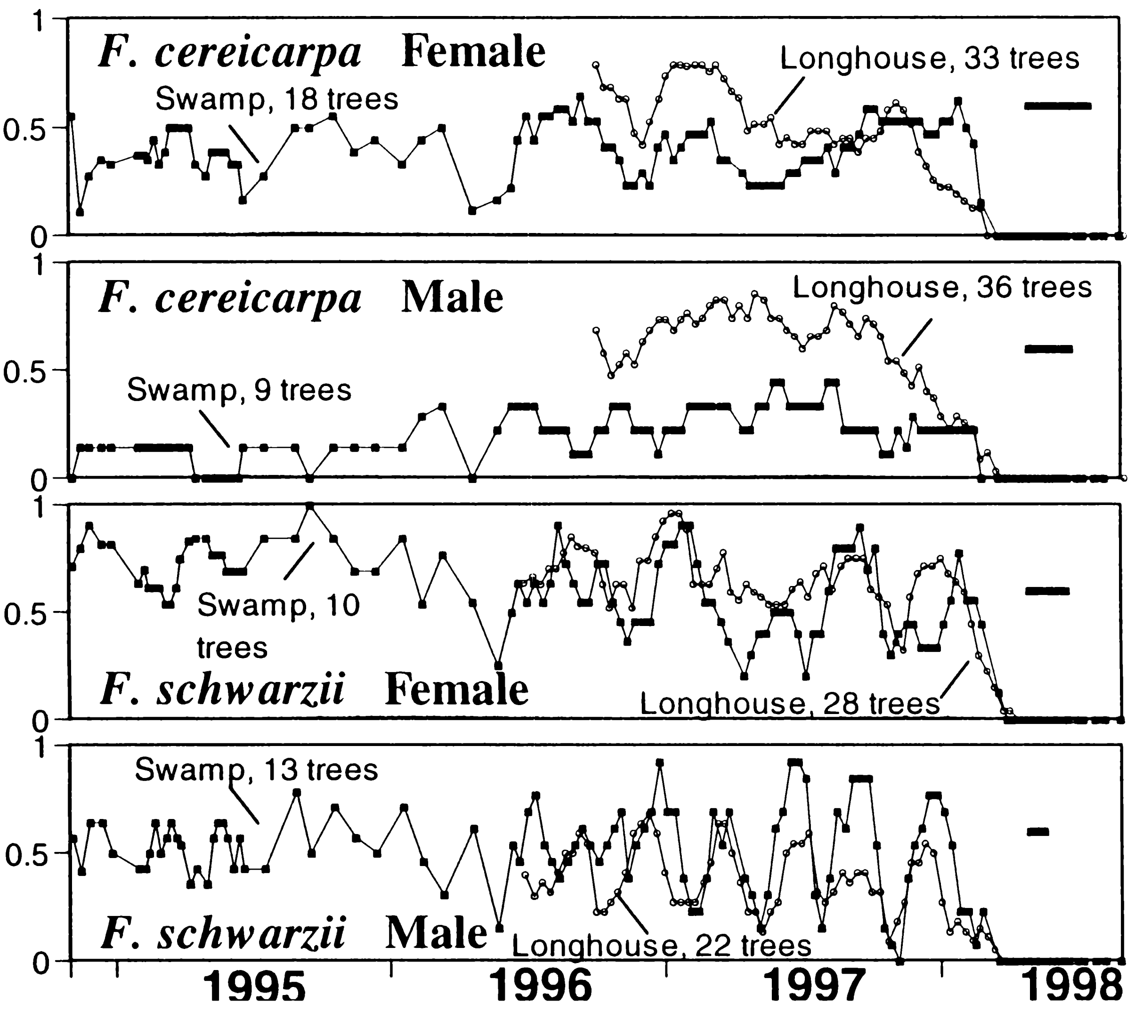

Figure 2-1 Mean proportion of trees with pollinated syconia at each census for *F. cereicarpa* and *F. schwarzii* in a small population (Swamp), Nov 1994 – Oct 1998, and a large population (Longhouse), Jun 1996 – Oct 1998. The solid bars indicate the approximate duration of individual pollinated syconia on the trees.

Both sexes of *F. cereicarpa* at the Swamp showed considerably variability in syconia production (note: only one male tree was reproductive until Feb 1996), however, the variance by quarter was not significant different across years (female: x^2=2.38 df=2, p>0.05; male: x^2=4.79, df=2, p>0.05; 1998 excluded, Kruskal-Wallis test) and mean was only significant different for males, which can be explained by an increase in the number of reproductively active trees over time (female: x^2=0.18, df=2, p>0.05; male: x^2=8.38, df=2, p<0.05, 1998 excluded, Kruskal-Wallis test). Also, there was no significant difference in variance by quarter between the Swamp and the larger Longhouse population over the same period (female: s=33, z=0.456, p>0.05; male: s=29, z=-0.091, p>0.05, 1998 excluded, Wilcoxon two sample test). The minor drought in Mar 1996 was accompanied by an obvious dip in the proportions of trees with pollinated syconia at the Swamp, though the levels recovered quickly. The drought in Mar 1997 apparently produced little response in either population. The severe drought in 1998 had induced the extinction of pollinating wasps by March, or two months after the onset (Fig. 2-2).

On the other hand, the proportion of female and male trees with pollinated syconia for *F. schwarzii* at the Swamp shows modest variability until Apr 1996 when both take a sharp dip following the drought. Thereafter, the proportions swing wildly both at the Swamp and at the Longhouse which was observed from Jun 1996. For the Swamp mean proportion by quarter did not vary significantly across years (female: x^2=3.96, df=2, p>0.05; male: x^2=0.15, df=2, p>0.05, 1998 excluded, Kruskal-Wallis test) but the variance of both sexes increased significantly from mid 1996 onwards (female: x^2=6.73, df=2 p<0.05; male: x^2=7.53, df=2, p<0.05, 1998 excluded, Kruskal-Wallis test). Again population size apparently had little effect on the variance, which was not significantly different over the same period in the Swamp and Longhouse populations (female: s=29, z=-1.52, p>0.05; male: s=28, z=-1.68, p>0.05, 1998 excluded, Wilcoxon two sample test). Although it is difficult to separate from the large variability, the 1997 drought was also followed by dips in the female Swamp population and both male populations in Mar and Apr 1997 respectively. Again, in 1998 both pollinator populations were extinct by March (Fig. 2-2). In neither species had the pollinators reinvaded the sites by Oct 1998.

Syconia production was highly significant correlated between sites for both sexes of both species, except female *F. cereicarpa* (Table 2-2). However, comparing species there were no significant correlations for either sex at both sites. Thus, species behaved differently but generally showed consistency at different sites. Interestingly, when comparing sexes there was no significant relationship at the Swamp while both species showed highly significant correlations at the Longhouse.

To investigate the level of synchrony within populations an auto-correlation analysis was conducted. At the Swamp neither species showed any significant auto-correlation in the period before the drought in Mar 1996. However, from Jun 1996 (start of 10 day censuses) male *F. schwarzii* showed a very highly significant auto-correlation with a period of 90 days at the Swamp and 100 days at the Longhouse (Fig. 2-3). Ninety days is equivalent to the crop period of an individual (Harrison,

Table 2-2 Correlations in the timing of syconia production for *F. cereicarpa* and *F. schwarzii* at two sites. Data on the proportion of trees with pollinated syconia at each census were compared by Kendall Rank Correlation, *tau* compared to a normal distribution (data after Feb. 1998 not included)

Between sites	*F. schwarzii*	*F. cereicarpa*
Male	0.420***	0.312**
Female	0.308**	-0.034ns
Between species	Male	Female
Swamp site	0.060ns	0.121ns
Longhouse site	0.080ns	0.029ns
Between sexes	Swamp site	Longhouse site
F. schwarzii	0.060ns	0.258**
F. cereicarpa	-0.100ns	0.373***

(ns p>0.05, * p<0.05, ** p<0.01, *** p<0.001)

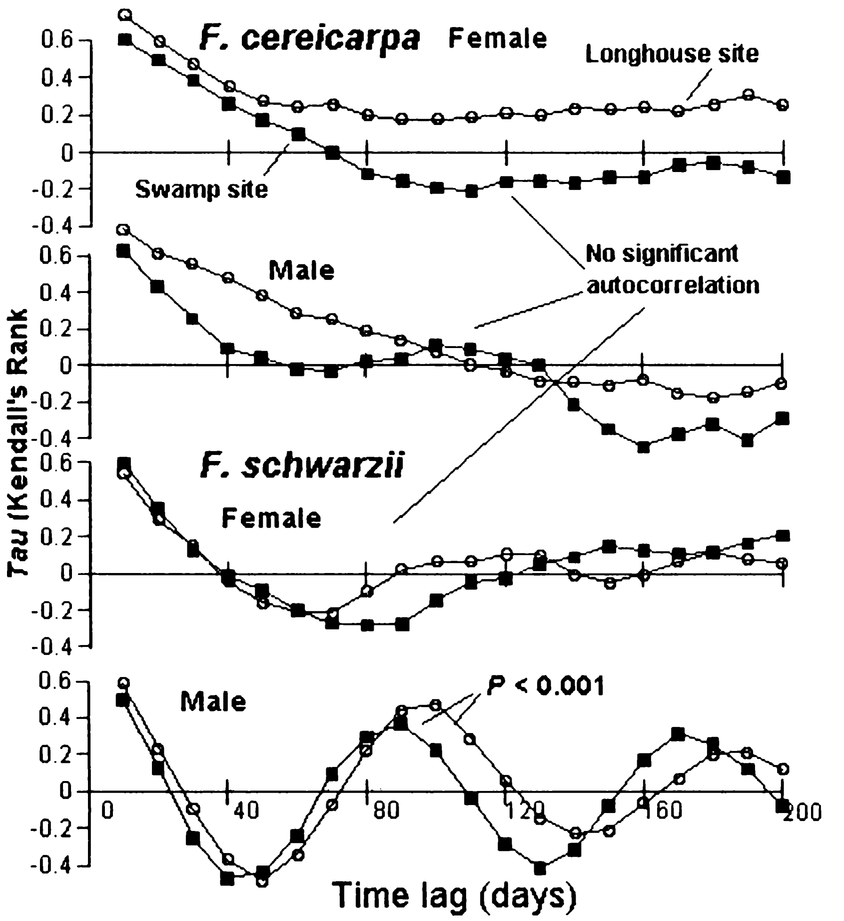

Figure 2-3 Auto-correlation of the proportion of trees with pollinated syconia at each census for *F. cereicarpa* and *F. schwarzii* in a small (Swamp) and large (Longhouse) population from Jun 1996 – Feb 1998. Kendall's Rank Correlation plotted against time lag (days), censuses were conducted every 10 days.

unpublished). Female *F. schwarzii* and both sexes of *F. cereicarpa* did not show any significant periodicity at either site.

2.3.3 *Rainfall, leaf production and syconia initiation*

Correlations between the leaf production, syconia initiation and rainfall, including time lag correlations of up to 50 days, were investigated (Table 2-3). Although some factors were significantly correlated there was no consistence between sites, or between sexes, contrary to the findings in Tables 2-1 & 2-2. Such inconsistent results possible reflect in part complicating factors, such as resource levels, but probably also qualitatively different responses when rainfall is limiting as to when it is abundant. When drought (30 day rainfall <100 mm) and non drought (30 day rainfall >100 mm) periods were compared highly consistent results were obtained. Thus, there was a highly significant reduction in the proportion of trees with new leaf during drought periods for both sexes of both species at each site. Likewise, there were highly significant reductions in the proportions of trees with immature syconia for both sexes of *F. cereicarpa* at each site (30 day delay), and a significant reduction for female *F. schwarzii* at each site (40 day delay). Only male *F. schwarzii* showed no significant difference between drought and non drought in the proportion of trees with immature syconia but this likely reflects the peaks and crashes generated by a strong internal rhythm following the first drought in Mar 1996.

Table 2-3: Correlation between leaf production, syconia initiation and rainfall in two species of dioecious fig at Lambir Hills National Park, Sarawak. Proportion of trees with new leaf and immature syconia by census, and rolling thirty-day rainfall totals compared by Kendall Rank Correlation, *tau* compared to a normal distribution. Drought (thirty-day rainfall total <100mm) compared with non drought (thirty-day rainfall total >=100mm) by Wilcoxon two sample test. Separate comparisons for Swamp and Longhouse sites. Mean monthly evaporation approx. = 100 mm.

			F. cereicarpa				*F. schwarzii*			
			Female		Male		Female		Male	
Swamp (Jan 1995 - Feb 1998)			**Delay**	***tau***	**Delay**	***tau***	**Delay**	***tau***	**Delay**	***tau***
New leaf	vs	Syconia initiation	10	0.275^{**}		ns		ns		ns
New Leaf	vs	Rainfall		ns		ns	40	-0.348^{**}	0	0.149^{*}
Syconia initiation	vs	Rainfall		ns	40	0.174^{*}	0	-0.206^{**}		ns
Longhouse (Jun 1996 - Feb 1998)										
New leaf	vs	Syconia initiation		ns		ns		ns		ns
New Leaf	vs	Rainfall		ns		ns		ns		ns
Syconia initiation	vs	Rainfall		ns		ns		ns	40	-0.193^{*}

Drought	**vs**	**Non drought**	*F. cereicarpa*				*F. schwarzii*			
			Female		Male		Female		Male	
Swamp (Jan 1995 - Feb 1998)			**s**	**z**	**s**	**z**	**s**	**z**	**s**	**z**
		New leaf	503	-3.294^{***}	517	-3.144^{**}	512	-3.223^{**}	348	-3.264^{**}
		Syconia initiation	623	-2.550^{**}_{a}	524	-3.429^{***}_{a}	597	-2.374^{*}_{b}	968	$0.832\mathrm{ns}_{b}$
Longhouse (Jun 1996 - Feb 1998)										
		New leaf	275	-3.904^{***}	247	-4.316^{***}	314	-3.71^{***}	367	-4.433^{***}
		Syconia initiation	220	-2.863^{**}_{a}	184	-3.489^{***}_{a}	357	-2.636^{**}_{b}	458	$-1.230\mathrm{ns}_{b}$

(ns $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$; a: 30 day delay, b: 40 day delay)

2.3.4 *Overlap in critical crop stages: male phase, female receptive and male receptive*

Plots of the total number of female receptive, male receptive and male phase syconia at each census for each species, for both periods of intensive study at the Swamp and at the Longhouse are shown in Fig. 2-4. Overlap of (i) male phase with female receptivity is indicative of male reproductive success and female pollination success, (ii) male phase with male receptivity is indicative of pollinator reproductive success and, (iii) female and male receptivity suggests potential competition between sexes for pollinators and the possibility for wasps to select male syconia. Inspection of the plots shows that all three situations occur frequently (Fig. 2-4). At the Swamp none of the parameters were significantly correlated in either species, but at the Longhouse male and female receptivity were correlated in both species and male phase with female receptivity in *F. cereicarpa* (Table 2-4). Brief consideration of the plots (Fig. 2-4) suggests that the inconsistency between the sites is caused by the large stochastic variation of these short crop phases in the smaller Swamp population, while at the Longhouse response to the droughts is most probably the factor causing the correlations.

At the Swamp wasp production and male receptivity in *F. cereicarpa* was sporadic, reflecting the very small number of male trees in the population, as evidenced by a much more stable production at the Longhouse (Fig. 2-4). In the case of *F. schwarzii*, female receptivity is more or less even over time, although at the Swamp it fluctuates reflecting a small number of trees in the population. The pattern of male

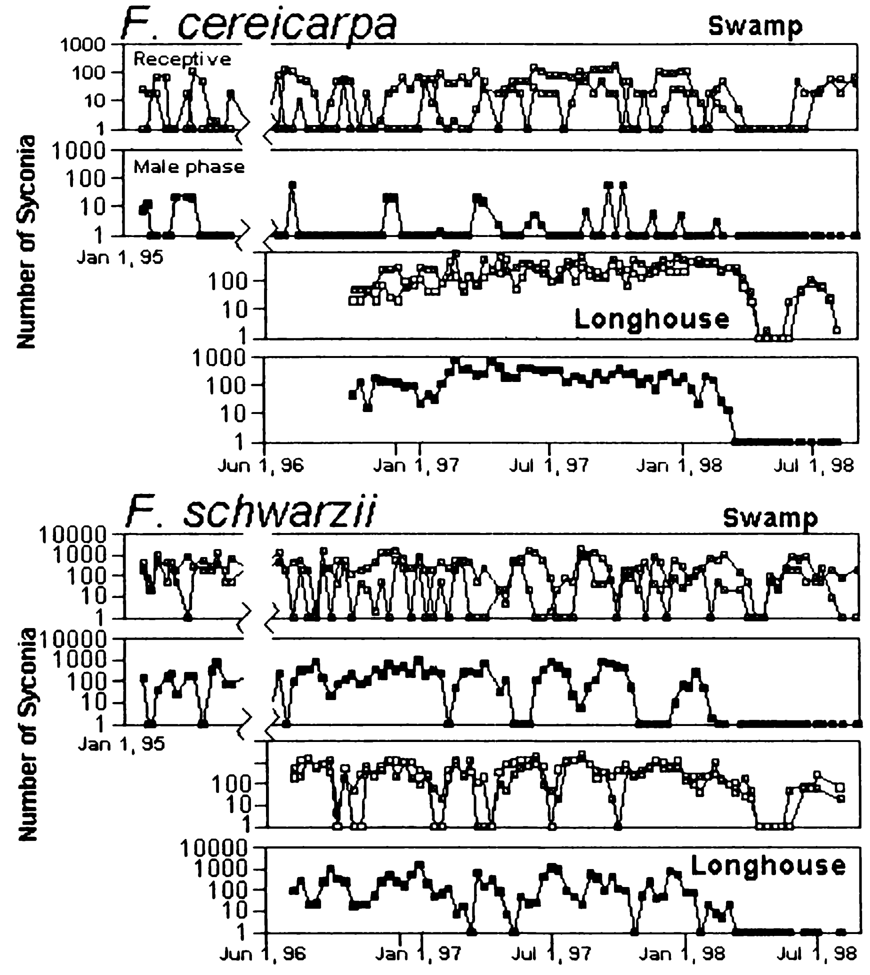

Figure 2-4 Total number of female receptive (o), male receptive ( ) and male phase syconia (■) at each census for *F. cereicarpa* and *F. schwarzii* at two sites, Jan 1995 – Oct 1998. For the Swamp only the periods of intensive census are shown, as monthly recording is insufficient to record these brief crop phases. Overlap of female and male receptivity with male phase (wasp production) is significant for the reproductive success of both fig trees and pollinators (see text for details).

Table 2-4 Overlap of critcal syconia developmental phases and correlation to wasp populations. Number of receptive syconia, male phase syconia and number of each wasp species caught on stick traps at each census compared by Kendall Rank Correlation, *tau* compared to a normal distribution.

		F. cereicarpa		*F. schwarzii*	
		Swamp	Longhouse	Swamp	Longhouse
Male receptivity	vs Female receptivity	0.146ns	0.285**	0.056ns	0.459***
Male phase	vs Female receptivity	0.106ns	0.201*	-0.022ns	0.024ns
Male phase	vs Male receptivity	-0.036ns	0.152ns	-0.038ns	0.119ns
Female receptivity	vs Pollinators on female trees	-0.103ns	#	0.117ns	#
Male receptivity	vs Pollinators on male trees	0.030ns	#	0.107ns	#
Male phase	vs Pollinators on female trees	0.154ns	#	0.243*	#
Male phase	vs Pollinators on male trees	0.074ns	#	0.427***	#
Pollintor	vs Non pollinator (male trees only)	0.561***	*Sycocarpus*	0.036ns	*Apocryptophagus*
				0.370***	*Philotrypesis*
				0.405***	*Apocrypta*

(ns p>0.05, * p<0.05, ** p<0.01, *** p<0.001)

receptivity and male phase, however, reflects the peaks and troughs in syconia production seen earlier (Fig. 2-2 & 2-4). During the drought in 1998, there was a substantial gap in the availability of both receptive syconia and male phase syconia (Fig. 2-4), caused by syconia withering in the dry conditions. This led to the extinction of the pollinator populations.

Syconia abortion rate (No. aborted/No. initiated) showed a highly significant negative correlation to total number of male phase syconia, for both sexes of both species (*F.* cereicarpa: female tau=-0.181, p<0.01, male tau=-0.201, p<0.01; F. *schwarzii*: female tau=-0.228, p<0.01, male tau=-0.331, p<0.01, data after Feb. 1998 not included, Kendal Rank Correlation). Thus, when wasps were not being produced in the local population pollination success was low.

2.3.5 Wasp arrivals at sticky traps

The captures of pollinators on yellow sticky traps at the Swamp reflected the availability of receptive syconia and production of wasps within the population (Fig. 2-5). As expected, pollinators were only occasionally captured in trees without receptive syconia and always in low numbers. However, at times of little or no wasp production within the population wasps were rarely caught even if receptive trees were present. Thus, for *F. schwarzii* pollinator captures were highly significantly correlated to number of male phase syconia but not to number of receptive syconia (Table 2-4). Nevertheless, a small number wasp arrivals were recorded when there was no wasp production within the population and with the infrequent wasp production in *F. cereicarpa* this led to a non significant result (Table 2-4).

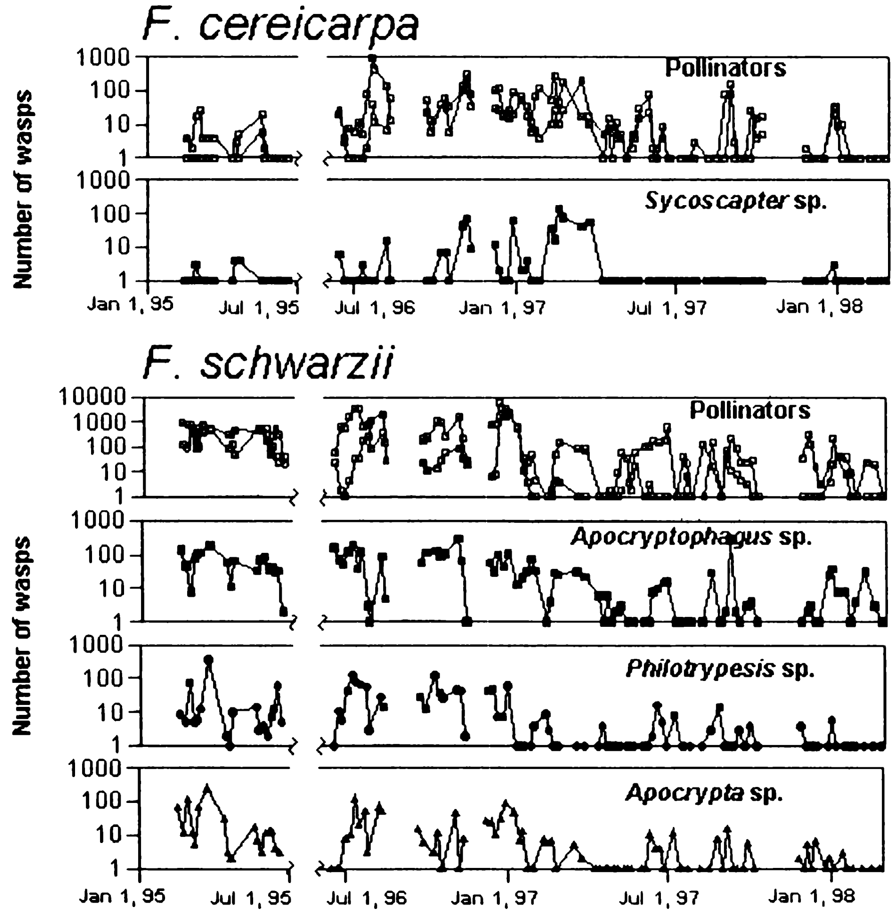

Figure 2-5 Total number of pollinators caught on yellow stick traps hung in female (o) and male (□) trees and non pollinators from traps in male trees by census, for *F. cereicarpa* and *F. schwarzii* at the Swamp. Two trapping periods are shown and gaps in data collection within the second period are indicated by breaks in the plotted lines.

The non pollinating galler, *Sycoscapter* sp. on *F. cereicarpa* was only captured when pollinators were also present, although it was only sporadically recorded and disappeared from the population from mid 1997 (Table 2-4 & Fig 2-5). However, *Apocryptophagus* sp. on *F. schwarzii* was not correlated to the dynamics of the pollinator. In fact, when pollinator populations were very low it was often the only wasp ovipositing on the syconia. The other non pollinators on *F. schwarzii*, *Philotrypesis* sp., a gall parasite, and *Apocrypta* sp., a parasitoid, initially also had dynamics similar to the pollinators on male trees. However, following a crash in the populations of all wasp species in Jan 1997 their populations never recovered. Both species were in fact extinct within the population for several months before sporadically re-invading. All non pollinators became extinct in the 1998 drought (Table 2-4 & Fig 2-5).

2.4 Discussion

2.4.1 Production of new leaf and syconia

Both the production of new leaf and syconia were continuous at the population level in the two dioecious fig species investigated (Fig. 2-1 & 2-2). However, while leaf production, a maintenance activity, was essentially similar between species and sexes, syconia production was very different, suggesting that selection for divergent reproductive strategies has occurred.

Leaf production was highly correlated between species and sexes, though there were some differences in amount (Table 2-1), and there was a highly significant reduction in leaf production during droughts (Table 2-3). Thus, both sexes of both species behaved in a similar way under normal conditions and in their response to drought. Given these species are closely related, found at the same sites and occupy similar pioneer habits, this result is perhaps not surprising, although previous studies have tended to reveal a range of responses (Windsor *et al.* 1989; Milton 1991; Compton 1993; Damstra *et al.* 1996; Spencer *et al.* 1996).

Syconia production in *F. cereicarpa* showed little difference across years or between small and large populations. Although the drought in 1996 caused a brief dip, the proportion of individuals with pollinated syconia was maintained at a constant high level, 50% or more in the larger population, until the end of 1997 (Fig. 2-2). Syconia production was significantly correlated between sites in male trees but not in females. The latter appears to be due to an early tailing off of syconia production in Nov/Dec 1997 at the Longhouse, which also explains the correlation between sexes at that site but not at the Swamp (Table 2-2 & Fig. 2-2). The cause of this is not clear, although it coincides with the onset of dry conditions before the drought in 1998. Syconia initiation was significantly reduced by drought but was otherwise stochastic with respect to rainfall (Table 2-3). Thus, the within crown asynchronous phenology of *F. cereicarpa* appeared to reduce variability in syconia production, even in a small population, and buffer against the effects of minor drought, although syconia initiation was affected.

The situation for *F. schwarzii* was quite different. Prior to the minor drought in 1996 the proportion of trees with pollinated syconia in the small Swamp population was relatively stable and maintained at a high level, roughly 50% in males and higher in females. However, there was a significant increase in the variance following the minor drought in 1996 (Fig 2-2). The highly significant correlation in syconia production between sites (Table 2-2) suggests that the peaks and crashes, triggered by the 1996 drought, followed an internal rhythm characteristic of the species. The fact that male trees had a highly significant periodicity equivalent to the crop period of an individual supports this (Fig. 2-3). Female trees did not become so synchronised hence no significant periodicity could be detected but inspection of the peaks also shows them separated by roughly the crop period of an individual (90 days, Fig. 2-2). The variance was not significantly different between small and large populations and importantly from the perspective of stability of the pollinator populations, the crashes in the proportion of male trees with pollinated syconia reached equivalent low levels (Fig 2-2). In fact, the pollinator population at the Swamp actually became extinct briefly in early Nov 1997 two full cycles of peaks and crashes following the second minor drought in Mar 1997, but reinvaded quickly. Thus, while the within crown synchrony but short periodicity of crops in *F. schwarzii* maintained a continuous and stable production of syconia under 'normal' conditions, it was clearly very sensitive to disruption by periods of stress such as drought.

The differing susceptibility of each species to disruption by drought may be explained by a simple mechanism. During drought, while trees were stressed, the initiation of new syconia was postponed (Table 2-3) but later stage syconia continued to develop. Hence, there was a queuing effect which in *F. schwarzii* led to a strong peak immediately following the drought, and successive peaks and crashes then followed from the strong internal fruiting rhythm of individuals reinforced by high rates of syconia abortion during each crash. The within crown asynchrony of *F. cereicarpa* on the other hand, increased the chance of more individuals having earlier stage syconia which developed over the drought period and also tended to stagger the initiation of syconia after the drought.

2.4.2 *Reproductive success of figs and pollinators*

A lack of correlation in the number of male phase to female receptive or male receptive syconia (Table 2-4) indicates that there is no population level co-ordination of these phases which might be adaptive to fig or pollinator reproductive success. This though is expected given the continuous fruiting phenology of these species and the aseasonal conditions, which provide for a stochastic but temporally even chance of reproductive success. It is also similar to the ancestral monoecious condition (Wharton *et al.* 1980; Milton *et al.* 1982; Bronstein 1988a; Windsor *et al.* 1989; Milton 1991; Compton 1993). In *F. schwarzii* one might expect the drought which synchronised the male trees and to some extent the females, to act as a cue so that peaks of male phase would overlap with female receptivity (situation (i) above) (Patel 1996). However, there was no correlation between these phases and in fact at the Longhouse male and female receptivity were highly correlated. Only for *F. cereicarpa* at the Longhouse was there any correlation between male phase and female receptivity. However, this appears to reflect a gradual decrease in the production of syconia in both male and female trees towards the end of 1997 rather than a short term co-ordination of phases (Fig 2-4).

The strong negative correlation between male phase and abortion rate, of both female and male syconia, in both species indicates that when few or no wasps are being produced within the local population pollination success is low. This is strong evidence that these relatively small groups of trees can be considered local populations. Nevertheless, the fact that sometimes low numbers of pollinators, especially of *F. cereicarpa*, were caught on sticky traps when there were no male phase trees in the Swamp population and that *F. schwarzii* recovered quickly from the first extinction of its pollinator, indicates that these populations are not completely isolated.

The potential for pollinators to select receptive male syconia in preference to female syconia (situation (iii) above) evidently exists most of the time in both species (Fig 2-4 & Table 2-4). The question of how this is evolutionarily stable when pollinators can only reproduce in male syconia has been raised (Kjellberg *et al.* 1987b). It was suggested that partial discrimination may be evolutionary stable when overlap is occasional (Patel *et al.* 1995). However, 'rush selection' (also considered by Patel *et al.* 1995), where pollinators simply enter the first receptive syconia, is the more likely mechanism when overlap is frequent as is the case here.

2.4.3 Pollinator and non pollinator population dynamics

The pollinator population dynamics deduced from the yellow sticky traps captures are highly correlated to wasp production in the population (Table 2-4). This is further indirect evidence that these small groups of trees can be considered local populations, at least in terms of the maintenance of the pollinator populations. Pollinators and non pollinating gallers depend on a similar resource, that of the gall ovules within receptive male syconia but often pollinator populations are much higher (Fig 2-5) (West & Herre 1994; Patel & McKey 1998). This may be explained by the fact that pollinators enter the syconia, and can quickly utilise the available gall ovules out-competing the non pollinators which oviposit through the syconia wall. In this case, we might expect the proportion of non pollinating gallers to increase when pollinator populations are low and this appears to be the case for *Apocryptophagus* sp. on *F. schwarzii* (Fig 2-5). The other non pollinators of *F. schwarzii* depend on the availability of the galls or larvae of the pollinator, or possibly *Apocryptophagus* sp., and initially their population dynamics mirrored fluctuations in the pollinator population (Table 2-4). However, their susceptibility to crashes in the pollinator population is self evident (Fig 2-5). The ability of these non pollinators to recover from population crashes may be limited due the time taken to locate and oviposit on suitable galls. On any tree these are only available for a short period and when there are only a few scattered pollinated syconia amongst many unpollinated ones, this may drastically reduce their fecundity.

2.4.4 *Aseasonality and seasonality in dioecious fig phenology*

Earlier I suggested that dioecious figs may have evolved to the existence of small populations in an aseasonal environment. The first prediction (1) that syconia production should be even throughout the year within these small populations, was borne out in the case of *F. cereicarpa,* and for *F. schwarzii* in the period before the 1996 drought. Furthermore, one of the main results shown above was that the species studied here do appear to belonged to relatively, but not completely, isolated small local populations as per the second prediction (2). Importantly, the size of the local population also had only a minimal effect on the stability of the pollinator population. In the case of *F. schwarzii* the small population was stable before 1996 and larger population suffered equally badly from the peaks and crashes after mid 1996. While in *F. cereicarpa* although the Swamp population, with only three mature male trees, suffered from sporadic adult pollinator production, the pollinator populations were stable until the 1998 drought. This suggests that, at least without the severe disruption of a drought, the threshold number of male trees required to maintain the pollinator populations is very low in these species.

The third prediction (3), that drought should have a substantial impact on pollinator population stability was true in the case of *F. schwarzii*, for minor droughts and both species in the case of a major drought.

In a study of dioecious fig phenology in relation to seasonality in southern India Patel (1996) came to the conclusion that one species, *F. exasperata,* with a synchronous phenology similar to *F. schwarzii* was adapted to a seasonally dry environment. The situation was also similar for *F. variegata* in a seasonal forest in Australia (Spencer *et al.* 1996) and appears to be true of some species in Hong Kong (Hill 1967). Clearly this does not agree well with the findings for *F. schwarzii* here. However, this conclusion was based on the fact that the main seasonal peak of male receptivity preceded the peak in female receptivity by a period equivalent to the development time of the wasp larvae. Thus, male trees were maximising the chances of wasps entering female receptive syconia (situation (i) above). In *F. schwarzii* overlap was stochastic and continuous, in agreement with adaptation to aseasonal conditions. Also, pollinator populations of *F. exasperata* were not stable within the observed populations (equivalent to the populations sizes observed in this study). Actual population size must have been considerably larger and given the very strong synchrony of the seasonal peak wasps may have been arriving from trees located far away in less seasonal conditions, as may occur in some monoecious figs (Bronstein 1989). So although superficially similar in having a synchronous phenology the ecology of *F. exasperata* is obviously quite different. Wasp dispersal, population size and timing of syconia production are obviously relatively malleable characters and in these two examples were adapted in directions predictable from the climatic environment. Interestingly, Patel had difficulty explaining out of season syconia production on male *F. exasperata*, when there are no receptive female syconia, and suggested it may be remnant of the ancestral monoecious condition. However, the results here suggest that it may simply be that *F. exasperata*, or a more recent dioecious ancestor, is found in more aseasonal conditions where year round fruiting is adaptive.

The second, asynchronous species *F. hispida*, studied by Patel (1996) appears to be very similar to *F. cereicarpa*. Syconia production was much more variable, however, this is expected if this phenology was poorly adapted to the seasonal conditions as Patel (1996) suggests.

3 Phenology of a common roadside fig in Sarawak

Summary – The phenology of a common dioecious fig (*Ficus fulva*, 25 female, 26 male trees) was studied at Lambir Hills National Park, Sarawak in relation to climate and sexual specialisation. Leaf phenology was strongly correlated between sexes. Trees dropped leaf during drought and initiated new leaf after the renewal of rain. Before the production of large crops trees shed their leaves and new leaf and syconia were initiated together. Syconia were produced in synchronous crops with asynchrony between trees maintaining a relative even production of syconia within the group. Syconia abortion on male trees, but not on females, was negatively correlated to the proportion of trees with male phase syconia. A severe drought in early 1998 disrupted the phenology thereafter. The duration of crop development was approximately twice as long on female trees than on males, and total syconia production was much higher on male trees. Plots of syconia diameter vs. dry weight suggest sexual specialisation in the investment profile during crop development. Male trees also sometimes produced a small crop immediately before a large crop, presumably to supply wasps for the main crop. Sexes had different growth strategies with male trees growing more as small individuals and slightly delaying reproduction. Diameter at breast height was significantly correlated to total syconia production in male trees but not in females. Syconia production was best predicted by canopy width.

3.1 Introduction

Dioecious figs are amongst the most common species in secondary habitats throughout Borneo, often constituting 50% or more of the individual plants in a forest (Corner 1940, *unpublished data*). Their individual dominance and the copious production of fruit on many species mean figs are an extremely valuable resource for vertebrate seed dispersers (Boon & Corlett 1989; Lambert & Marshall 1991; Tan *et al.* 1998), and thus for forest succession and the re-assembly of mature forest (Compton *et al.* 1994b; Thornton 1994; Thornton 1996). Furthermore, the intricate mutualism between figs and their pollinators permits a detailed examination of the constraints and benefits of different ecological traits, which may reflect on how such an extraordinary diversity of species, and individual dominance in secondary habitats, could have evolved (Janzen 1979b; Compton 1993; Herre 1996; Patel 1996; Chapter 2).

Moreover, in dioecious figs separate individuals perform female and male roles. Hence, seed production has been de-coupled from wasp and pollen production permitting sexual specialisation (Lambert 1992; Corlett 1993; Patel & McKey 1998). The evolution of sexual dimorphism in plants with hermaphrodite ancestors provides a window to understanding the changes associated with evolution of dioecy and the selective pressures on each sex (Lloyd & Webb 1977; Bawa 1980; Cox 1981). The constraints and possible benefits of a system in which the sexual roles are still coupled, as in the monoecious figs, can also then be better understood (Bronstein 1992; Herre 1996).

In this study I investigate the influence of climate, especially rainfall, and sexual specialisation on the phenology of a common roadside fig, *Ficus fulva*, in Sarawak.

3.2 Materials and Methods

3.2.1 Species and Study Site

Ficus fulva Reinw. ex Bl. (Subgenus *Ficus*, sect. *Ficus*, Corner 1965) is a heliophilic dioecious fig tree up to approximately 10 m tall, which bears its syconia along smaller branches and at the twigs. It is found from lower Thailand through Sumatra, Java, Borneo, Sulawesi and Timor (Corner 1965). It is pollinated by *Blastophaga compacta* Weibes (Wiebes 1993) and has two undescribed non pollinating fig wasps, *Apocryptophagus* sp. and *Philotrypesis* sp (*unpublished data*). The seed dispersers are small, open space birds, especially the Yellow-vented bulbul (*Pycnonotus goiavier*) in LHNP (Shanahan 1997), though bats have been known to take *F. fulva* fruit on the Krakatoa Islands (Compton *et al.* 1988). *F. fulva* is very common on small ridges along roadsides and amongst sifting cultivation in Sarawak. In the primary forest at LHNP it is restricted to large landslide gaps (LaFrankie *et al.* 1995).

A group of *F. fulva* individuals around the park headquarters area and for approximately 500 m along the road back towards Miri were marked and observed from April 1997 – Sept 1998. Twenty-four male trees and 23 female trees were initially included, but a further two individuals of each sex found amongst the other trees were added June 1997 and one individual of each sex died in early April 1998 from drought stress. Thirteen immature trees, which did not produce mature crops and hence their sex could not be determined were also observed. One male tree and four immature individuals were killed when a section of the road was widened in February 1998. The data on all individuals are included in the analysis. Other *F. fulva* individuals were present along the road in both directions from the area under observation.

Rainfall data for the park for the period 1988 – 1998 was obtained from the Telecom Malaysia tower located in the park, while temperature data for the period 1991 – 1998 was obtained from Miri Airport 30 km from the research site.

3.2.2 Field observation

Phenology censuses were conducted every 10 days until June 1998 and then twice per month until September 1998. At each census the amount of leaf, as a proportion of the crown, and proportion of new leaf, old leaf and senile leaf were recorded using a 1 – 4 scale (1 <25%, 25%>2<50%, 50%>3<75%, 4>75%). Number of syconia were estimated on a log scale with three sub-groupings, thus 1 – 3, 4 – 6, 7 – 9, 10 – 39, 40 – 69 and so on. Crop developmental stage was assigned as Immature, Receptive, Pollinated and Fruit/Male (Galil 1973). Crop stage was assessed by outward appearance through binoculars. This was adequate to assess all stages except receptivity. When a crop was suspected of being receptive a small number (3 – 5) of syconia were sampled by climbing the tree and cutting off a twig. However, this was not always possible and the exact timing and duration of receptivity had to be estimated from the occurrence of other phases. The proportion of syconia at each developmental stage was estimated on a similar 1 – 4 scale to the leaf data.

The diameter at breast height was measured on 15 April 1997 (DBH1) and again on 27 June 1998 (DBH2) using a forester's diameter tape and the number of stems recorded. For trees with more than one stem a combined DBH was calculated from the sum of the basal area of each stem. On 7 August 1998 tree height (using a measuring pole), canopy width (measured by tape at the widest point) and crown illumination index (5 crown completely exposed; 4 full overhead light (>90%), some or all lateral light blocked; 3 some overhead light (10-90%) or lateral light (<10%); 2.5 high lateral light; 2 medium lateral light; 1.5 low lateral light; 1 no direct light, Clark & Clark 1992) were measured.

Between December 1997 and February 1998, 20 syconia were collected from selected trees at each census, their diameters and wet weights measured. Syconia were dried in individual envelopes in a constant temperature drying oven and their dry weights measured 5 days later. When possible syconia were sampled from the same crop until the crop disappeared from the tree.

3.2.3 Data analysis

Data were analysed using *SAS* (*SAS Institute Inc* 1985, PROC SUMMARY and PROC CORR). I calculated the proportions of trees in each sex with new leaf, flushing (>25% of crown consisting of new leaf), senile leaf, the mean proportion of bare crown (leaf drop), and with syconia at each developmental stage, for each census. In aseasonal equatorial climates leaf exchange often occurs continuously, especially in pioneer species such as this, but with occasional peaks in leaf renewal generally referred to as flushing (eg Reich 1995). Hence, the distinction in this analysis between the presence of new leaf on an individual and flushing, defined as when more than 25% of the crown consisted of new leaf. An asynchrony index of the syconia on each tree at each census was calculated as follows: one crop stage present=0, two neighbouring crop stages present=1, immature overlapping with pollinated or fruit/male phases (i.e. two cohorts present on the same tree)=2, receptive overlapping with fruit/male (on the same tree)=3. The latter indicates substantial overlap between cohorts on the same tree and is significant because of the potential for wasps to enter syconia on the same tree in male individuals. The mean crop asynchrony index was then calculated by census. The proportion of syconia aborted was calculated for each receptive crop (Previous crop size – Present crop size) / Previous crop size. A crop was taken to be receptive if it had receptive syconia on either the previous or present date. The mean proportion of syconia aborted was then calculated by census. Kendall Rank correlation was used to compare these parameters and the 30 day rolling rainfall totals by census. Delayed correlations of up to 60 days at ten day intervals were investigated.

In calculating the duration of crop phases, those recorded at only one census, as often occurred for receptive and fruit/male, were assumed to be 5 days. Otherwise, they were taken from the first date recorded to the last. The pollinated phase generally overlapped completely with the fruit/male phase and often with the receptive phase. The period between crop initiation was calculated from date of the start of one crop until the start of the next on an individual tree and the period between crop finishings was calculated likewise between the ends of completed crops. The duration of each phase for each crop was calculated by individual and then the mean duration for each sex generated. Crop sizes were calculated only for crops which finished development.

Total syconia production, mean crop size, number of crops initiated, and the proportion of census dates with new leaf and flushing were calculated by individual over the entire study period. These were then correlated with DBH2, growth (DBH2-DBH1), canopy width and canopy illumination index by sex (Pearson correlation). Growth and proportional growth ((DBH2-DBH1)/DBH1) were correlated with DBH1 by sex. Growth could not be calculated for trees which died during the study or for trees which lost stems. Proportional factors were arcsin transformed.

3.3 Results

3.3.1 Influence of climate and population level phenology

(i) Leaf phenology

Both sexes of *F. fulva* produced new leaf year round though the proportion of trees with new leaf varied greatly (Fig. 3-1). The peaks in new leaf and flushing correspond to periods of new rain after droughts in Feb – Mar 1997 and Jan – Apr 1998 (Fig. 1-3) and reflect leaf renewal after a large amount of leaf drop occurred during the drought period (Fig. 3-1). Leaf drop showed a highly significant negative correlation with rainfall (Table 3-1a). Leaf renewal, however, was not significantly correlated to rainfall except for a slight negative correlation with flushing on male

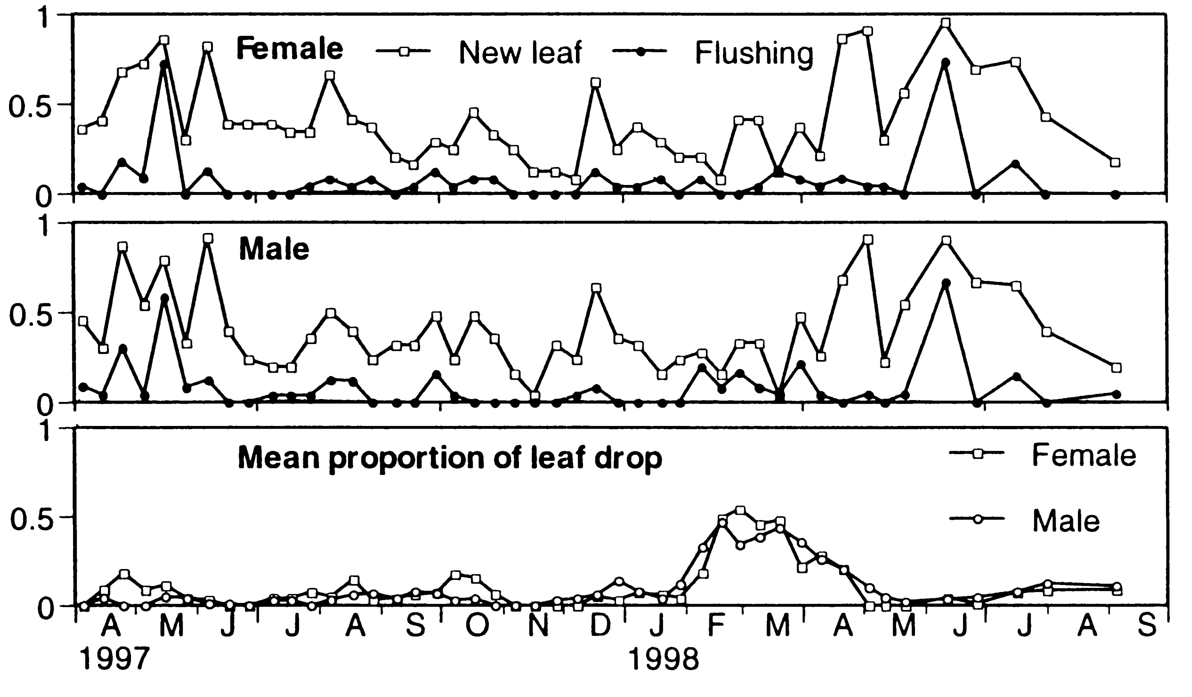

Figure 3-1 Proportion of female and male trees with new leaf present and flushing (>25% of crown consists of new leaf) and the mean proportion of leaf drop (bare crown) on female and male trees by census.

Table 2-1 Correlations in the timing of leaf production for *F. cereicarpa* and *F. schwarzii* at two sites. Data on the proportion of trees with new leaf present (New Leaf) and with >25% of the crown consisting of new leaf (Flushing) at each census were compared by Kendall Rank Correlation, *tau* compared to a normal distribution (data after Feb. 1998 not included).

Between sites		*F. schwarzii*	*F. cereicarpa*
	New leaf	0.431***	0.573***
	Flushing	0.247 ns	0.167 ns
Between species		Longhouse site	Swamp site
	New leaf	0.494***	0.322**
	Flushing	0.433**	0.154 ns
Between sexes		Longhouse site	Swamp site
F. schwarzii	New leaf	0.758***	0.485***
	Flushing	0.597***	0.495***
F. cereicarpa	New leaf	0.800***	0.401***
	Flushing	0.627***	0.359**

(ns p>0.05, * p<0.05, ** p<0.01, *** p<0.001)

trees. New leaf, flushing and leaf drop were all significantly correlated between sexes (Table 3-1c). At the end of the study a heavy caterpillar infestation (*pers. obs.*) caused another slight increase in leaf drop and possibly affected leaf renewal.

(ii) Syconia phenology

The proportion of female trees with pollinated syconia remained at a relatively constant level of around 0.4 until the onset of drought in Jan 1998 (Fig. 3-2). By contrast, on males trees the proportion of individuals with pollinated syconia showed a slight cyclic undulation before the drought, indicating that the trees were slightly synchronised at the population level. There were no pollinated syconia on either female or male trees from the end of Mar to mid Apr 1998, indicating a temporary extinction of the pollinator wasps within the observed group, and although pollinators returned thereafter the proportions of individuals with pollinated syconia never recovered their pre-drought levels. Mean crop asynchrony was generally very low (mean female=0.12, male=0.12, max. value is 3), indicating that crops are generally highly synchronous within a tree (Fig 3-2). The occasional small peaks, however, show that sometimes cohort overlap occurs.

Syconia initiation was significantly negatively correlated to rainfall in both sexes (Table 3-1a). This indicates a tendency to initiate crops following dry weather. There was a delay of 30 days on female trees with respect to male trees (although syconia initiation was still correlated between sexes, Table 3-1c). Syconia initiation was also highly correlated to flushing. Before the initiation of large crops trees would

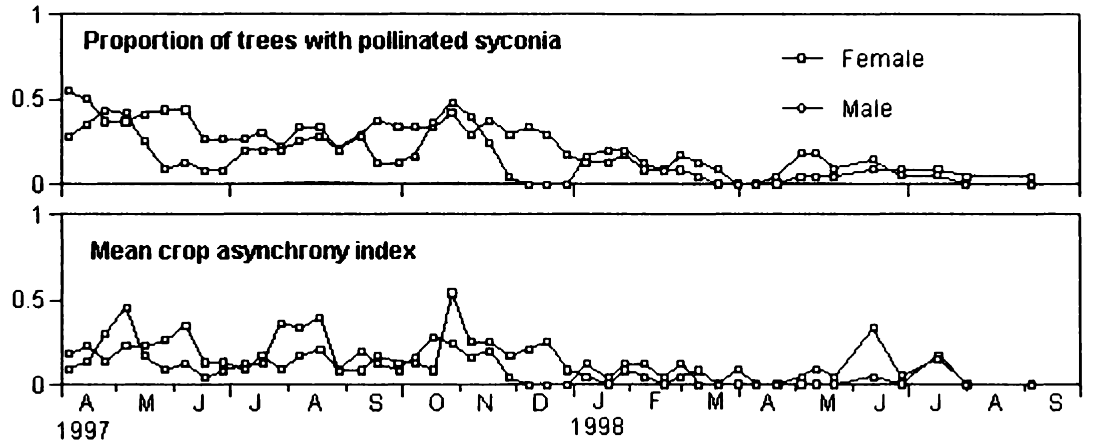

Figure 3-2 Proportion of female and male trees with pollinated syconia and the mean crop asynchrony index by census. The proportion of pollinated syconia is the best indicator of syconia production amongst the observed trees, because it includes all stages of wasp larvae or seed developing on the trees. The mean crop asynchrony index has a maximum value of 3 and reflects the degree of stage / cohort overlap on an individual (see Materials and Methods section).

shed all their leaves and the bare twigs would then renew leaf and initiate syconia simultaneously.

The proportion of trees of either sex with receptive syconia was generally low (Fig. 3-3), reflecting the normally short duration of this phase, but generally there were some receptive individuals present, and there was a large degree of overlap between the sexes. There were always male phase syconia present until just prior to the drought in 1998, indicating a continuous production of pollinating wasps within the observed group of trees. Likewise, the production of fruit on female trees was almost continuous up until the drought and the pollinator extinction. Following the drought a sudden production of crops produced a peak in receptive trees but, although some syconia were pollinated, wasp and fruit production did not recover the pre-drought levels (Fig. 3-3). The proportion of trees with male phase syconia and with receptive syconia on either male or female trees was not significantly correlated (Table 3-1c), indicating that there was no co-ordination of these phases at the population level. There was a significant negative correlation between the proportion of trees with male phase syconia and syconia abortion on male trees but not on female trees (Table 3-1b). The significant correlation with rainfall on male trees possibly reflects the high levels of abortion through lack of pollinators and high rainfall following the drought in 1998.

3.3.2 Sexual specialisation

(i) Parameter means compared between sexes

Table 3-2 compares the phenology of female and male trees. The number of crops initiated on female trees was slightly higher but the proportion of these which

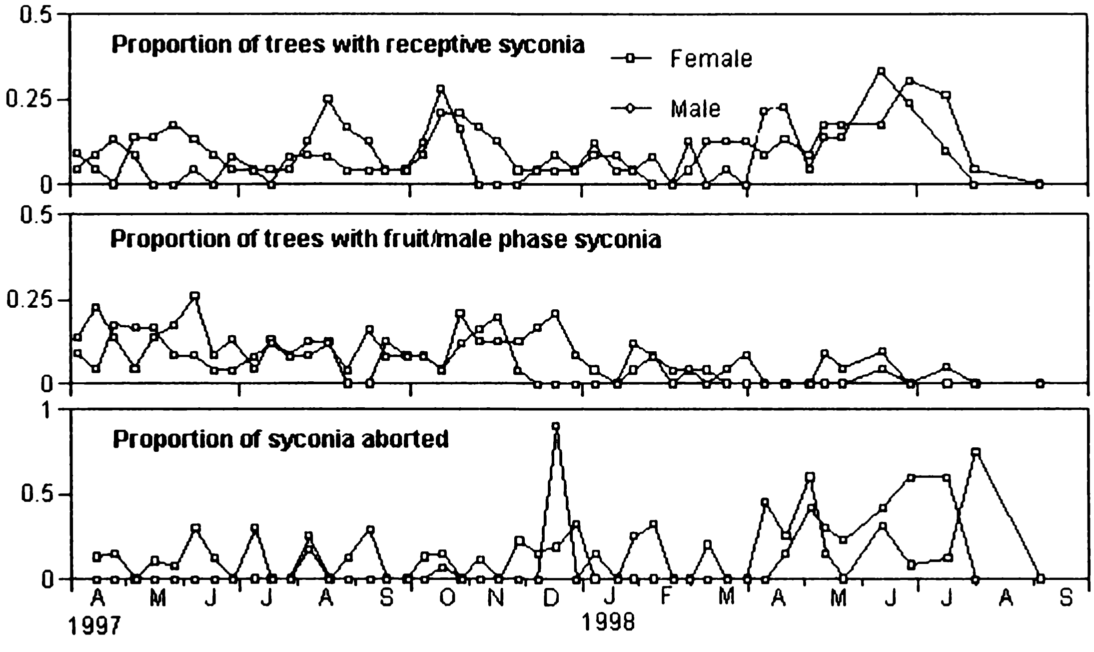

Figure 3-3 Proportion of female and male trees with receptive syconia, fruit/male phase syconia and the proportion of syconia aborted by census.

finished was considerable lower than on male trees. The duration of the immature phase was similar on male and female trees but all other phases were longer on female trees. The extension of receptivity on female trees probably reflects delayed pollination but as mentioned above recording this phase accurately was difficult. Thereafter, syconia take approximately twice as long to develop on female trees than on male trees. There is an interesting difference in the plot of syconia diameter versus dry weight between female and male trees (Fig. 3-4). On female trees dry weight increases linearly with syconia diameter while on male trees it appears to increase exponentially, especially when the courses of individual crops are followed. The crowding of many points on the female plot reflects the slower maturation of syconia.

The mean period between crop initiations, or crop finishings, however, was only marginally longer on female trees indicating these had a shorter interval between successive crops when the tree was not bearing any syconia. However, a frequency distribution plot of the period between crop initiations shows an interesting difference between the sexes (Fig. 3-5). The graph is strongly left skewed in females but has a bimodal distribution in males. Short periods on female trees are caused when the previous crop fails to develop and hence the tree produces the next one quickly afterwards. However, male trees often initiated a small crop of 20 to 50 syconia just before a large crop. There was then a long interval until the next pair of crops thus producing a bimodal distribution.

The mean crop size and total number of syconia were both much higher on male trees (Table 3-2).

Table 2-2 Correlations in the timing of syconia production for *F. cereicarpa* and *F. schwarzii* at two sites. Data on the proportion of trees with pollinated syconia at each census were compared by Kendall Rank Correlation, *tau* compared to a normal distribution (data after Feb. 1998 not included)

Between sites	*F. schwarzii*	*F. cereicarpa*
Male	0.420***	0.312**
Female	0.308**	-0.034ns
Between species	Male	Female
Swamp site	0.060ns	0.121ns
Longhouse site	0.080ns	0.029ns
Between sexes	Swamp site	Longhouse site
F. schwarzii	0.060ns	0.258**
F. cereicarpa	-0.100ns	0.373***

(ns $p>0.05$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$)

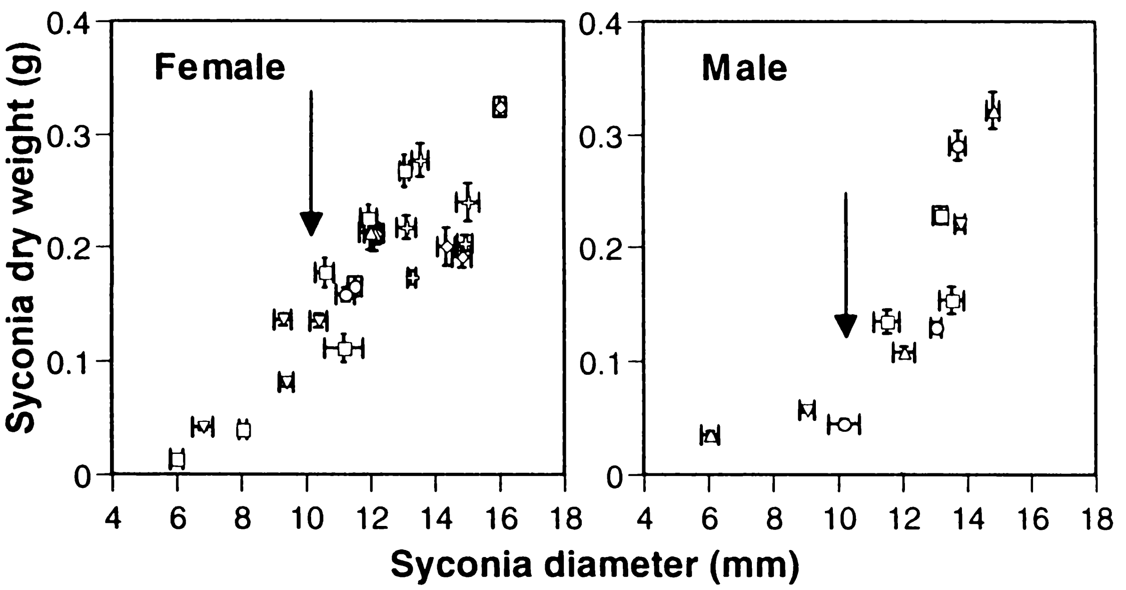

Figure 3-4 A plot of syconia diameter versus syconia dry weight for female and male trees (data points with SE bars). □ indicates single unconnected samplings. Each of the other symbols represent samples taken from the same crop at 10 day intervals. The arrows indicate the approximate size at receptivity.

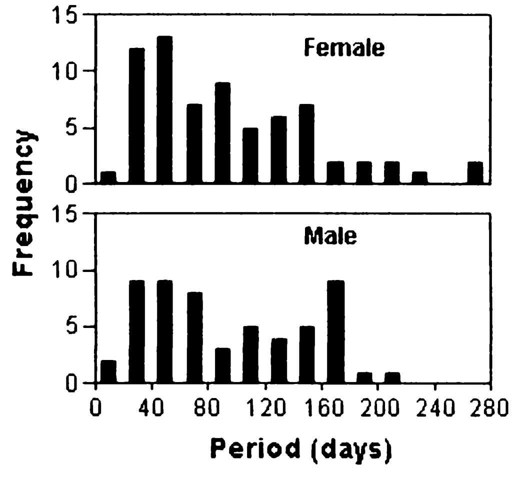

Figure 3-5 Frequency distribution of the period between crop initiations on female and male trees. Each datum is generated from the duration in days between date of the start of one crop to the date of the start of the following crop on an individual tree.

Amongst the tree characteristics measured female and male trees differed little except in stem mortality, which was higher in male trees. One male stem and the 4 immature stems which died were due to the road widening. Growth appears to have been higher in male trees but the very large variation obscures the result. Growth and proportional growth were significantly negatively correlated to DBH1 in male trees (Pearson's r, growth= -0.452, proportional growth= -0.488, p<0.05, n=21), but not in female trees (Pearson's r, growth= -0.167, proportional growth= -0.069, p>0.05, n=21), indicating that while larger male trees grew more slowly than smaller ones, in female trees growth did not decrease with increasing size. As expected immature individuals were much smaller but growth was not any higher except of one individual which grew from 63 mm to 131, or more than doubled in diameter, in the 14 months between measurements.

The mean size of the three smallest and largest individuals was different in female and male trees (Female, mean min.=37mm, max.=148mm; Male mean min.=46mm, max.=174mm). Female trees were smaller at both minimum and maximum ends of the range which suggests that female trees start reproducing at a smaller diameter and reach a smaller maximum diameter than male trees. However, a larger sample of trees would need to be measured to establish this relationship more concretely.

(ii) Individual tree characteristics and phenology compared by sex

An analysis of the correlation between tree characteristics and phenology generally produced good agreement between sexes (Table 3-3). DBH was significantly

Table 3-3 Individual level analysis of syconia and leaf production in *F. fulva* at Lambir Hills National Park. Diameter at breast height (DBH), diameter growth, canopy width and Canopy Illumination index (CI) were correlated with total number of syconia produced, mean crop size and number of crops finished, and with the proportion of census dates an individual had new leaf present and was flushing (>25% of crown).

			DBH	Growth	Canopy width	CI
Female	25	Total syconia production	0.347ns	-0.010ns	0.564**	0.037ns
		Mean crop size	0.191ns	-0.100ns	0.451*	0.044ns
		Number of crops finished	0.450*	0.307ns	0.390ns	0.219ns
		New leaf	0.510*	0.624**	0.471*	0.044ns
		Flushing	0.128ns	-0.128ns	0.073ns	0.204ns
Male	26	Total syconia production	0.484*	-0.130ns	0.596**	-0.051ns
		Mean crop size	0.373ns	-0.164ns	0.503**	-0.096ns
		Number of crops finished	0.132ns	-0.111ns	0.127ns	0.086ns
		New leaf	0.485*	0.050ns	0.332ns	-0.114ns
		Flushing	0.044ns	-0.184ns	-0.002ns	-0.083ns

(Pearson correlation coefficients given, ns, $p>0.05$, * $p<0.05$, ** $p<0.01$)

correlated with total syconia production in male trees but not in female trees. Although, canopy width rather than DBH was the best predictor of mean crop size and total syconia production in both sexes. The strong correlation between total syconia production and canopy width comes as no surprise given that the latter is indicative of both the area of canopy available intercept sunlight for photosynthesis and also of the number of twigs on which syconia can develop. The proportion of census dates with new leaf present was significantly correlation with DBH, growth and canopy width in females but only with DBH in males.

3.4 Discussion

3.4.1 Influence of climate and population level phenology

(i)Leaf phenology

Although some new leaf was present at all times, the pattern of leaf phenology was strongly influenced by drought and the initiation of large crops of syconia. Drought caused a significant increase in leaf drop which was then followed by new leaf production with the renewal of rain (Fig. 1-3 & 3-1). The severe drought in early 1998 clearly caused substantial water stress, inducing the death of two individuals, and by dropping leaf the trees attempted to alleviate water loss. Following the drought, although new leaf was produced, the trees under observation did not appear to recover well. Syconia production did not return to its pre-drought levels and the very heavy caterpillar infestation observed at the end of the study probably reflected ailing trees.

Usually rates of herbivore attack are very low in figs (*pers. obs.*), which are protected by copious latex. However, latex production is expensive (Farrell *et al.* 1991) hence when plants are stressed they may not be able to allocate sufficient resources to its production. In *F. variegata* in northern Australia (Spencer *et al.* 1996) leaf production was strongly correlated to rainfall seasonality, and in another study at LHNP (Chapter 2) leaf renewal showed a strong negative correlation to drought. The correlation of leaf flushing and syconia initiation almost certainly reflects a physiologically based constraint on species, such as *F. fulva*, which produce their syconia at the tips of the twigs. At least one other species found in LHNP, *F. aurata*, which is found in similar habitats and produces syconia at the twig tips, also had correlated leaf flushing and syconia initiation (*unpublished data*), but in other cauliflorous species they were unrelated (Chapter 2).

(ii) Syconia production

F. fulva produced highly synchronous crops within a tree but between tree asynchrony maintained an almost continuous production of both male phase syconia (pollinator production) and fruit within the group until the severe drought in early 1998. The cyclic undulation in the proportion of trees with pollinated syconia on male trees (Fig. 3-2) indicates a slight synchrony between trees but it was not sufficient to cause breaks in pollinator production within the group. Crop initiation was negatively correlated to rainfall reflecting the large numbers of crops started during and immediately following the drought. However, the proportion of pollinated syconia was not significantly correlated with rainfall, which is in contrast to other studies in dioecious fig phenology where syconia production showed a strong correlation to rainfall seasonality (Hill 1967; Patel 1996; Spencer *et al.* 1996), and to drought at LHNP (Chapter 2).

Inter-tree asynchrony also produce broad overlap between syconia receptivity on female and male trees and pollinator production within the group. Overlap in receptivity on female and male trees allows wasps to select male syconia, where they can reproduce, over female syconia, where they cannot. The longer duration of receptivity recorded on female trees (Table 3-2) may reflect some partial preference (Patel *et al.* 1995) for male syconia. However, considerable caution is warranted given the difficulties in accurately assessing the duration of the receptive phase, as explained above, and the possibility of other causes such as the potential for male trees to provide their own pollinators. Wasp preference can only be properly assessed by wasp choice experiments.

There was an overall lack of group level co-ordination between trees with male phase syconia and receptive phase syconia on female trees, but the correlation between syconia initiation and rainfall was delayed 30 days on female trees relative to male trees. Previously, a delay in peak initiation of syconia on female trees relative to male trees in strongly seasonal environments has been interpreted as adaptive for the male figs to pollinate female syconia (male reproductive success and female pollination success) (Patel 1996; Spencer *et al.* 1996). The initiation of syconia in *F. fulva* after the drought may thus be similar to the behaviour of dioecious figs in strongly seasonal environments. However, adult wasp life spans are very short so unless pollinator production actually overlaps with receptivity on female trees there is no advantage, and caution should be exercised in reading in an adaptive interpretation.

The almost continuous production of wasps within the group may have important implications for the population size of genetically interacting trees in *F. fulva*. Although wasps may be able to disperse long distances, as has been demonstrated in some monoecious figs in Panama (Nason *et al.* 1996), the continuous proximity of trees releasing pollinators suggests these sources may swamp out more distant sources, as was observed occasionally in the Panamanian figs. The negative correlation between syconia abortion and the proportion of trees with male phase syconia within the group also suggests that local wasp sources may be important. Syconia abortion can be caused by resource limitation, pollen limitation or possibly disease although evidence for the latter was never found. However, separating these components is difficult because often unpollinated and pollinated syconia are aborted from a crop at the same time, and very few aborted syconia were found in the field until the time of the drought. The low rates of abortion until Dec 1997 likely reflect mostly resource limitation while the later peaks, pollen limitation (Fig. 3-3). In this instance, local pollinator shortages or a regional paucity cannot be separated but clearly, a genetic study of *F. fulva* and other dioecious figs in LHNP similar to the one on Panamanian figs would be very interesting.

3.4.2 Sexual specialisation

The reproductive phenology of *F. fulva* demonstrated considerable sexual specialisation. Crop development was approximately twice as long on female trees.

Other studies of dioecious fig phenology have also tended to demonstrate a longer development time of syconia on female trees than on male trees (Hill 1967; Corlett 1987; Corlett 1993; Chou & Yeh 1995; Patel & McKey 1998). In this study a longer receptive phase on female trees most likely reflects pollinator shortage, rather than any advantage to extend the receptive phase especially as wasp production in the group was almost continuous. It may well reflect the ability of male tree to supply their own pollinating wasps. Patel (1998) suggested longer development of syconia on female trees was due to the greater number of ovaries and fleshier syconia which would require more investment. However, in *F. fulva* crop periodicity was similar, hence the number of crops produced per unit time was almost the same on female and male trees. On male trees physiological development of the wasp larvae may be inflexible (Galil 1977) thus preventing a more gradual investment by the fig, or it could be a predator avoidance strategy reducing the time window available for non pollinating wasps to oviposit on the figs. Non pollinating wasps have longer adult life spans than the pollinators (*unpublished data*) and, because they oviposit from outside the fig, they are able to move from one syconia to the next. Alternatively, longer development on female trees may reflect selection to sample a wider range of seed dispersal environments (Patel & McKey 1998), given the greater variation in syconia development and hence a longer fruit phase. However, one could also anticipate selection on male trees to sample a wider range of pollination environments. Crop development on monoecious figs is generally short (3 – 8 weeks)(Patel & McKey 1998, *unpublished data*) more similar to the development time on male trees, suggesting that it is the syconia development on female trees has become extended (Patel & McKey 1998). This would also suggest that in monoecious figs female reproductive fitness may be compromised by the duration of wasp larval development.

Female and male trees also differed in their syconia investment profiles (Fig. 3-4). In female trees syconia dry weight increased linearly with syconia diameter suggesting that investment in syconia is independent of crop phase. On male trees initial investment was low up until approximately the time of receptivity and thereafter increased rapidly. It appears therefore that males are minimising investment until pollination has occurred. This strategy may reflect the much larger crop sizes on male trees preventing a heavy loss of resources from abortion if pollinator shortages occur.

The large number of crops with short periods (Fig. 3-5) and the lower proportion of crops which finished (Table 3-2) on female trees reflects a large number of crops which were initiated but failed to develop at the time of the drought. This excepted, female trees produced crops of similar size with even periodicity. The tendency for male trees to initiate a small crop immediately prior to a large one, producing a bimodality in crop periodicity (Fig. 3-5), is interesting. The obvious suggestion is that the trees are kick-starting the main crop by investing in the small crop to produce the pollinators for the main crop. In monoecious figs self pollination carries a double cost of inbreeding depression and reduced pollen flow, but in dioecious figs only the latter applies. Hence, it is quite possible to envisage how investing in a small number of syconia to guarantee pollination of the main crop may be advantageous. The male phases of the small crops often did overlap with receptivity in the larger crop, but there were also occasions on which the phases did not appear to overlap. Interestingly, the smaller crops were generally produced on the main branches, back from the tips, similar to the situation described in *F. carica* (Valdeyron & Lloyd 1979), and possibly reflecting the need to decouple the syconia production from leaf renewal which would occur with the main crop.

Figs are iteroparious plants. *F. fulva* produces on average three crops per year and individuals are reproductive for at least five years (*pers. obs.*). Given the degree of sexual specialisation in syconia phenology, we might expect to find sexual specialisation in life history strategy. The smaller mean minimum diameters in female trees, and the fact that female trees did not show any significant growth/diameter relationship, suggests that female trees start reproducing at a smaller diameter and then continue growing at a constant rate. While male trees appear to delay starting reproduction until they reach a larger diameter and grow quickly as small trees but increasingly slowly as they reach a large size. This difference in growth strategy between sexes has two possible explanations. If mortality is size independent in female trees but higher in smaller individuals for male trees then higher investment in growth until a larger size is reached would be selected in males. The data here were insufficient to test this hypothesis although most stem mortality was amongst smaller stems in both sexes. If however, a larger crop size were advantageous for male trees then again investment in growth until a larger size is reached would be selected (Charnov 1982), and given the much larger mean crop size on male trees this seems likely. The lack of a good correlation between DBH and mean crop size is misleading because of the tendency for male trees to produce small crops before the main crop. DBH was significantly correlated to total syconia production in male trees. In female trees, however, total syconia production was independent of DBH which is predicted if there is selection for a continuous rate of investment in reproduction and growth. Size related sexual specialisation is reported from *Arisaema* (e.g. Kinoshita 1986) which actually change from small male to large female plants, but appears uncommon elsewhere in the plant kingdom.

It is perhaps surprising that in *F. fulva* sexual specialisation in leaf phenology, or other tree characteristics and their relationship to syconia production were not found. A difference in, for example, canopy illumination index might have indicated different habitat preferences in female and male trees. The short duration of the study, however, may have prevented their elucidation. This could be an interesting line of enquiry in future studies.

4 Repercussions of El Niño: Drought causes extinction and the breakdown of mutualism in Borneo

Summary - Figs and their species specific pollinators, the fig wasps (Agaonidae), have co-evolved one of the most intricate interactions found in nature in which the fig wasps, in return for pollination services, raise their offspring in the fig inflorescence. Fig wasps, however, have very short adult lives and hence are dependent on the near continuous production of inflorescences to maintain their populations. From January to March 1998 northern Borneo suffered a very severe drought linked to the El Niño/Southern Oscillation event of 1997/1998. This caused a substantial break in the production of inflorescences on dioecious figs and led to the local extinction of their pollinators at Lambir Hills National Park, Sarawak. Most pollinators had not re-colonised six months after the drought and, given the high level of endemism and wide extent of the drought, some species may be totally extinct. Cascading effects on vertebrate seed dispersers, for which figs are often regarded as keystone resources, and the tree species dependant on their services are also likely. This has considerable implications for the maintenance of biodiversity under a scenario of climate change and greater climatic extremes.

4.1 Introduction

The lowland Dipterocarp forests of South East Asia are the oldest and most diverse rain forests on earth. Their antiquity and the favourableness of a permanently humid, equatorial climate with little seasonality has been implicated in the development of such high biological diversity (Whitmore 1984). Nevertheless, occasional severe droughts are considered to have a major impact on the ecology of these forests (Whitmore 1984; Ashton 1993; Walsh 1996; Whitmore 1998), especially through increased tree mortality caused by water stress (Becker *et al.* 1998; Tyree *et al.* 1998) and largely anthropogenic fires (Leighton & Wirawan 1986; Woods 1989). The response of animal populations, such as herbivores, pollinators or seed dispersers, dependent on plant resources to these catastrophic disturbances is hardly known. Although, with increasing isolation of populations into small relic patches of forest, the possibility of a gradual loss of biodiversity and even ecosystem collapse if co-evolved interactions disintegrate has been recognised (Whitmore 1998). Recent predictions of worsening and more frequent drought induced by global warming (Meehl 1997; Guilderson & Schrag 1998; Salafsky 1998; Timmermann *et al.* 1999) are therefore of serious concern.

The figs are one of the most diverse and ecologically important genera in lowland dipterocarp forests (Corner 1940; Lambert & Marshall 1991), but while their unique seed predator/pollinator pollination system provides them with an excellent service, it also has its constraints. Adult female pollinators have an extremely short life span (≈1 day Kjellberg *et al.* 1988, *unpublished data*). Thus, within a population of fig trees the cycling of the pollinator population from one crop to the next can only be maintained if syconia production is nearly continuous. Consequently, figs are restricted to habitats, or climates, where this is possible. It is also the continuous production of fruit, especially when there is a dearth of other seasonal fruits, that makes figs so valuable to vertebrate seed dispersers (Terborgh 1986; Lambert & Marshall 1991).

The unprecedented El Niño/Southern Oscillation ENSO event of 1997/98 (Webster & Palmer 1997) induced the longest drought on record for north-western Borneo (Fig. 4-1), considerably more severe than that caused by the 1982/83 ENSO which previously held this accolade (Leighton & Wirawan 1986; Woods 1989). Large areas of northern Borneo, including north Sarawak, Brunei, Sabah and parts of Kalimantan experienced widespread fires and a haze crisis. As in the 1982/83 ENSO (Leighton & Wirawan 1986; Woods 1989) drought killed many mature trees (Nakagawa *et al. in press*). Of 576 individuals in 305 plant families under phenological observation at LHNP only 29 individuals died over a five year period between Jan 1993 – Jan 1998, mostly from tree falls, but a further 63 died during 1998 (Canopy Biology Program Sarawak, *unpublished data*). Drought can be presumed to be the main cause as other large scale factors, such as fire, wind throw or insect attack, can be ruled out. On the summit of Mt Kinabalu, the only other site with published observations of the 1998 drought thus far, a very high mortality across all types of vegetation was recorded, again suggesting the impact was more severe than in previous droughts and also demonstrating that it affected a wide geographical area and altitudinal range (Kitayama *et al.* 1999; Kudo & Kitayama 1999).

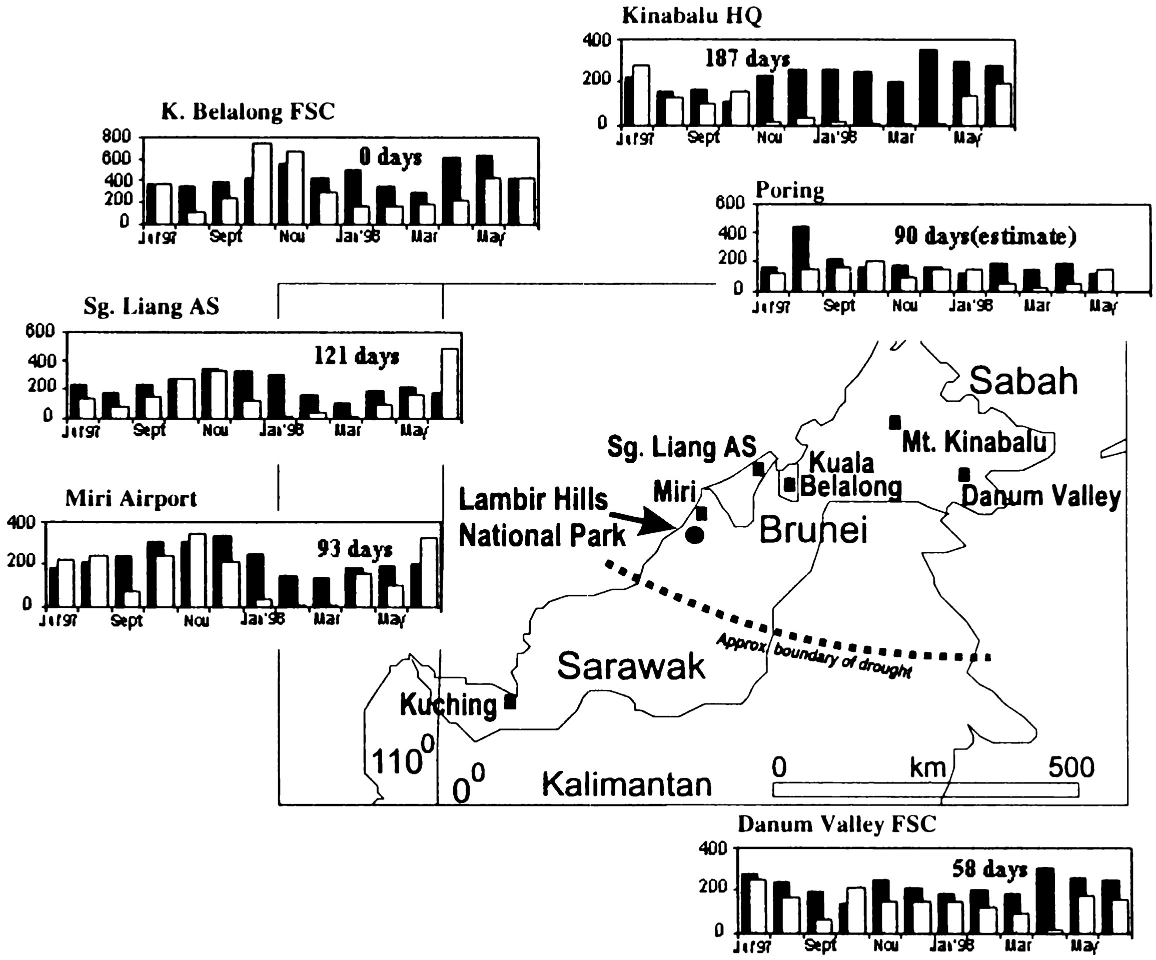

Figure 4-1 Map of northern Borneo showing the area affected by the 1998 drought. For each of the six sites monthly rainfall (, mm) from July 1997, the start of the drought, to June 1998 is compared to the long term monthly means (■). The number of days for which the thirty day rolling rainfall totals remained below 100 mm is also given (mean monthly evaporation is approx. 100 mm, Whitmore 1984). Two sites for Mt. Kinabalu are given HQ (1560 m) and Poring (550 m) (Kitayama 1999). Other data from Malaysian Meteorological Service, Brunei Meteorological Service, K. Belalong Field Studies Centre and Danum Valley Field Studies Centre. From Jan 1998 – Mar 1998 only 7% of the mean rainfall over the same three months fell at LHNP. Comparison to published accounts of long term rainfall records from Miri indicate that this was the worst drought since records began or at least 70 years, and a drought of such severity would be expected less than once in 350 years (Nakagawa *et al. in press*; Harrison *in submission*).

4.2 Materials and Methods

Observations of fig phenology in LHNP started in Oct 1994 and from Mar 1997 to Oct 1998 twenty-five species of dioecious fig and twelve species of monoecious fig were included in the phenology census (species identification followed Corner 1965). However, for many species the sample sizes were small, often only one or two mature individuals, as reflected their densities in and around the national park. Censuses were conducted approximately every ten days and at each census the leaf and syconia phenology were recorded. The total number (log scale with three subdivisions) of syconia and proportion at each developmental stage (immature, receptive, pollinated, male / fruit (Galil 1973) were assessed. For species with accessible syconia, including one climber, *F. punctata*, for which ladder systems were used, the crop stage could be assessed directly by sampling and opening or by inspection of the external appearance and evidence such as pollinator wings in the ostiole bracts. For most climbers and hemi-epiphytes with inaccessible syconia the developmental stage was assessed through binoculars, which cannot be considered reliable for short phases such as the receptive and wasp producing phases, but was sufficient to recognise immature, mid to late stage pollinated and fruit phases.

SAS (PROC SUMMARY, *SAS Institute Inc* 1985) was used to generate total numbers of syconia at each crop stage for each species by census. This paper deals only with the impact of the severe drought in 1998 on the fig wasp populations.

4.3 Results

The number of pollinated syconia is indicative of the presence of adult pollinators at the time of crop receptivity and the population size of wasp larvae developing on the trees (males only for dioecious figs) under observation. Fig. 4-2 shows the number of pollinated syconia on eight selected species of (a) dioecious and (b) monoecious figs from Jan 1997 to Oct 1998, when observations ceased. The numbers of pollinated syconia on dioecious figs, though variable in some species/sexes reflecting the initiation of syconia, indicate that the pollinator populations were stable up until the beginning of the drought in Jan 1998. However, all pollinators of these figs were locally extinct by end-Mar 1998, two and a half months after the onset of dry conditions (Fig. 4-2a). Trees dropped leaves, failed to initiate new syconia, and even pollinated syconia withered. The gap in the availability of receptive syconia this caused was over two months in these species, or approximately twice the total life span of the pollinators. The non pollinating wasp communities of these figs, some of which can retain syconia on the trees in the absence of pollinators, also became extinct at this time.

In seven out of the eight species shown here the pollinators had not re-colonised by Oct 1998, despite the availability of receptive syconia in all species from Apr 1998 onwards. Although small sample size precludes more detailed comment, none of the other seventeen species of dioecious figs under observation bore pollinated syconia at this time. By contrast, in the monoecious figs (Fig 4-2b) although few individuals bore syconia at the end of Mar 1998, wasps were immediately available

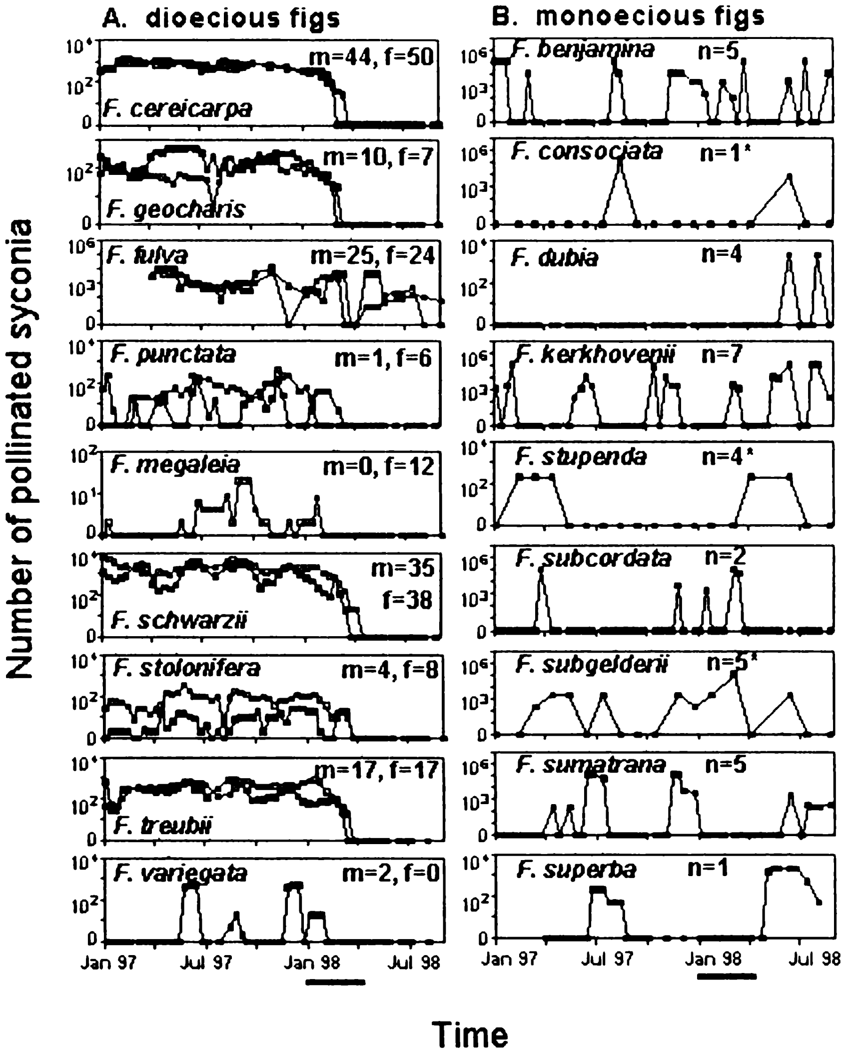

Figure 4-2 Number of pollinated syconia at each census on (a) dioecious (• male trees (m), □ female trees (f)) and (b) monoecious figs at LHNP. Pollinated syconia are indicative of (1) the presence of pollinating wasps at the time of crop receptivity and (2) the population of wasp larvae developing within the observed fig population, male trees only for dioecious figs. If syconia are not pollinated they are eventually aborted. Phenology censuses were conducted approximately every ten days (* indicates monthly censusing). Sample sizes are given on the figure. The bar below the time axis indicates the drought period.

when crops were initiated after the drought and hence crops were pollinated. In one species, *F. benjamina*, there were low rates of pollination amongst the first crops produced but more than 10% of the syconia were always pollinated.

4.4 Discussion

These results clearly demonstrate that in the eight species of dioecious figs at LHNP with stable wasp populations prior to 1998 all pollinators became locally extinct during the severe drought in early 1998, and from the observations of the seventeen other species it is probable that their wasps also became extinct at this time. Furthermore, in only one of the twenty-five species of dioecious figs under observation, *F. fulva* a very common roadside species, did the pollinators re-colonise before Oct 1998. Though in two other species, *F. schwarzii* and *F. treubii*, the pollinators had returned by Apr 1999 one year after the end of the drought (Shanahan *pers. comm.*). Occasional observations of other dioecious figs elsewhere in Sarawak (*pers. obs.*), Brunei (Jousselin *pers. comm.*) and Sabah (Mt Kinabalu) (Kimura *pers. comm.*), further suggest that pollinator extinctions were widespread, and covered most areas of Borneo affected by the drought.

Of the 40 species of dioecious figs found at LHNP, four species are endemic to northern Borneo, while the figure for the total flora is thought to be 15 species (Corner 1965). It is quite possible that the pollinators of some of these species may be completely extinct. As fig wasps are species specific pollinators their extinction ultimately means the extinction of the corresponding fig. The extremely high specificity of the fig – fig pollinator interaction makes invasion by the pollinators of other fig species seem very unlikely, though it is an intriguing possibility (Kerdelhue & Rasplus 1996a).

When the fig pollinator is not available crops go unpollinated and consequently there is no fruit production. Yet fig fruit have often been regarded as keystone resources for vertebrate seed dispersers (Terborgh 1986; Lambert & Marshall 1991). Although detailed studies of frugivory at dioecious figs are generally lacking, fruit production in many of these figs is continuous within small groups of trees (Fig 2a) (Corlett 1987; Corlett 1993; Chapter 2 & 3) and this, coupled with a general paucity of other fruits in the understorey (Loiselle & Blake 1999), suggests that they are an important resource for vertebrate seed dispersers. Small fruit bats are known to be largely dependant on dioecious figs (Boon & Corlett 1989; Tan *et al.* 1998), and in LHNP evidence of feeding on *F. schwarzii* by small fruit bats was regularly found and the bats often disturbed when walking around (*pers. obs.*). Since the drought, however, they have disappeared from this site and are scarce elsewhere in the park (Shanahan *pers. comm.*). These fruit bats are important seed dispersers and ultimately there may be a knock on effect on other tree species dependent on their services (Boon & Corlett 1989; Tan *et al.* 1998).

In an interesting contrast to the dioecious figs, monoecious fig pollinator populations seemed little affected by the drought. Very low densities, and hence small sample sizes, and sporadic crop production make the stability of the pollinator populations before the drought difficult to assess but syconia abortion from a lack of pollination was very rare, and immediately after the 1998 drought pollinators were available for all species which initiated crops.

Although the threshold fig population required to maintain their pollinators is particularly high in these monoecious figs, because of their intermittent fruiting, pollinators disperse long distances so populations are connected over very wide areas (Bronstein & Hossaert McKey 1995; Nason *et al.* 1996). When pollinators became locally extinct in Florida fig populations following Hurrican Andrew, as in LHNP they were available almost immediately after the initiation of new crops (Bronstein & Hossaert McKey 1995). These monoecious figs were also all large hemi-epiphytes and may be pre-adapted to drought as they often suffer acute water stress during their young epiphytic phase (Holbrook & Putz 1996). This is partly supported by the fact that none of the trees lost their leaves. By contrast, dioecious figs tend to be small pioneers, in open habitats, or climbers and are clearly prone to drought conditions. There is also some evidence that wasp dispersal is limited but that they stabilise the pollinator populations by more frequent fruiting and / or greater crop asynchrony (Corlett 1987; Corlett 1993; Kameyama *et al. in press*; Chapter 2).

In the dioecious figs it is possible that local extinction of pollinating wasps followed by a gradual re-colonisation from unaffected areas has occurred previously in Borneo, whenever there have been severe droughts. However, two worrying aspects need to be considered.

Firstly, the 97/98 ENSO event and the drought it induced are the strongest yet recorded and if the predictions of worsening and more frequent droughts (Meehl 1997;

Guilderson & Schrag 1998; Timmermann *et al.* 1999) are borne out it does not bode well for dioecious figs or the organisms dependent upon them.

Secondly, recent forest fragmentation may also have played a role as LHNP, like most remaining forest in the region, is a small patch (6500 ha) amongst scrubby secondary forest and palm plantations. Although the densities of dioecious figs, as pioneer plants, are often very high in the secondary forest (Corner 1940; *unpublished data*), the higher surface runoff and open canopy exacerbate drought conditions (Whitmore 1984). Over large areas reduced evapotranspiration may even disrupt local climatic cycles leading to lower precipitation (Salati *et al.* 1986). For example, in Kuala Belalong, Brunei where there are still significant areas of intact forest (>50 000 ha) the effects of drought were less severe, with monthly rainfall never dropping below 100 mm (Fig. 4-1). Significantly, in at least one species of dioecious fig at this site the pollinator wasps did not become extinct, although pollination rates were low (Jousselin *pers. comm.*). Hence, its possible that large areas of forest mitigated against droughts in the past. Furthermore, even if, as one would expect, most of these pollinator populations gradually recover from areas not affected by the drought, the impact on their vertebrate dispersers will be worsened by the small size and isolation of the remaining forest fragments.

Much of the considerable discussion about species conservation and extinction has concentrated on the viability of different population sizes (e.g. Soule & Wilcox 1980), especially of large rare species with high emotive value. However, in this case the local extinction of several extremely common species occurred when a single catastrophic event simply precluded reproduction for a period longer than the life span of an individual. Species with such brief life spans may not have so much apparent worth for conservation but if, as seen here, this also leads the disruption of keystone interactions upon which vertebrate populations depend then a gradual erosion of biodiversity can be expected.

5 Conclusions

Tropical rain forests occur where there are constant high temperatures and rainfall. More important than total rainfall, however, is it distribution throughout the year and most tropical regions experience at least a brief dry season (Whitmore 1998). The phenology of tropical trees is largely influenced by the length of this dry season, with phenology becoming less synchronised and more dependent on endogenous rhythms as the length of the dry season diminishes (van Schaik *et al.* 1993; Reich 1995). This has obvious implications for organisms dependent on plant resources. In more seasonal forests herbivores and pollinators must co-ordinate their lifecycles to the variable but predictable availability of resources (Aide 1988; Aiello 1992; Aide 1993). Whereas in more aseasonal forests there is less variability in amount of resources but these are generally also less predictable (Coley 1998). The tropical forests of South East Asia are the most aseasonal, but occasional droughts provide the opportunity to investigate the influence of unpredictable climatic variability. Moreover, in figs the strong coupling between pollinator populations and fig phenology, that results from the high specificity of the fig – fig wasp interaction and short adult life-span of the pollinators, enables one to interpret easily the impacts of different phenological strategies on fig and pollinator reproductive success.

The dioecious figs studied in Chapter 2, while similar in their leaf phenology, revealed large differences in reproductive phenology. Yet both could still be interpreted as being adaptive to aseasonal conditions. Leaf and syconia production were continuous but were affected by drought, with a decrease in leaf and syconia production during periods of low rainfall and an increase thereafter. Moreover, in syconia production there was no adaptive co-ordination of critical crop phases. Pollinator and non pollinator population dynamics were correlated to the production of wasps within each of the observed groups which was also correlated to fig pollination success. This suggests that patches of trees under observation were small semi-isolated populations. Each of the predictions for adaptation to aseasonal conditions, continuous but asynchronous syconia production in both female and male populations, disruption of phenology by drought and evidence for small populations, were thus borne out. Comparison to studies of dioecious figs in seasonal environments (Patel 1996; Spencer *et al.* 1996) further underlines the variability in phenological strategies and illustrates how malleable phenology and related traits are to local climatic conditions.

Drought had a significant effect on the phenology and thus the stability of the pollinator populations for both species, but *F. schwarzii* was more susceptible to minor droughts because its synchronous crop production and strong internal periodicity reinforced the initial disruption

With *F. fulva* in Chapter 3 synchrony of syconia within a tree but asynchrony between trees, and a relatively high frequency of crop production, maintained an almost continuous production of pollinator wasps and fruit within a small number of trees. However, again severe drought had a very significant influence on the phenology causing leaf drop and disrupting syconia production. This type of phenology, and the fact that there was possibly an adaptive response to drought with female trees delaying the initiation of syconia relative to males, is similar to the situation reported from seasonal sites (Patel 1996; Spencer *et al.* 1996).

As more species are studied in different environments and in various phylogenetic lineages a clearer picture will emerge as to the constraints and selective pressures acting on each species. Other biotic factors, especially the seed disperser syndrome, will also influence the phenological strategy. For example, most bird dispersed figs appear to have a highly synchronous phenology, while those dispersed by terrestrial mammals appear to have an asynchronous phenology (Shanahan 1997; unpublished data). To paraphrase Janzen (1979) we shall then be able to define various ways of being a fig, and how so many figs are able to co-exist.

F. fulva demonstrated considerable sexual specialisation in reproductive phenology and growth, but not in leaf phenology and other tree characteristics. Six aspects of sexual specialisation were recognised: (1) timing/frequency of syconia initiation, (2) crop size, (3) crop development time, (4) syconia investment profile, (5) the ability of male trees to supply their own pollinators and (6) a sex dependent growth strategy. Each of these indicates differing selection pressures acting on female and male roles and suggests a possible route for the evolution of dioecy from monoecy, which has occurred at least twice and possibly three times in figs (Berg 1989). It also points to a compromise between the sexual roles in the monoecious system. Yet 50% of the fig species world wide, and 30% where this study took place, are monoecious. So where are the advantages of the monoecious system?

In Chapter 4 we evidenced the local extinction of the pollinators of dioecious figs at LHNP during a severe drought. This demonstrates the vulnerability of tropical forests to catastrophic disturbance. These species, their fig hosts being pioneer plants, were incredibly common yet they became locally extinct because the drought prevented reproduction for longer than the life-span of an individual. Moreover, when keystone interactions such as these breakdown we can expect considerable disruption of the forest ecosystem and an associated lost of biodiversity. Hence, if the increasing frequency and severity of droughts predicted to occur with global warming are borne out, we can expect many more species to become extinct (Lips 1998; Pounds *et al.* 1999).

Scientists have finally agreed that global warming is both occurring and is caused by human impacts. It is also clear that it is the extremes of climate, and not the relatively small mean temperature rises, which will have the most significant biological impacts (Coley 1998). It is now essential to mitigate against these impacts by increasing the size of reserves and managing the matrix between them to serve as corridors or valuable secondary habitat (Phillips 1997; Bawa & Dayanandan 1998), as well as addressing the source of the problem and reducing carbon emissions (Martin 1996).

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---林冠に1日座って、飛び交う虫や鳥を
眺め、動物が植物と織りなす巧妙な共生
の一端をかいま見る。その時、畏敬の念
をもって、それ自体の、ありのままの価
値を理解できる心を私たちはもちたい。

井上　民二

（動物たちの地球110号より）

"...... sitting in the forest canopy for a day, watching the insects and birds flying past, we glimpse upon a part of the intricate relationships which animals and plants have woven so supremely.

"At moments like this, in awe of the nature of these things, we wish we could have the heart to understand them."

Tamiji Inoue